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A PHYLOGENY AND REVISION OF THE CADDISFLY GENUS Ceraclea (TRICHOPTERA, LEPTOCERIDAE)

By John C. Morse

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A PHYLOGENY AND REVISION OF THE CADDISFLY GENUS *Ceraclea* (TRICHOPTERA, LEPTOCERIDAE)[1, 2, 3].

By

John C. Morse[4]

ABSTRACT

The caddisfly genus *Ceraclea* Stephens is redefined to include 89 known species previously assigned to the genus *Athripsodes* Billberg. The two genera make up the tribe Athripsodini.

Three main lineages are recognized in *Ceraclea*, including the nominate subgenus and the subgenera *Athripsodina* Kimmins and *Pseudoleptocerus* Ulmer. Four species groups are identified in the subgenus *Ceraclea* and eight species groups in the subgenus *Athripsodina*. The African subgenus *Pseudoleptocerus* is not studied here in detail.

Descriptions, illustrations, and keys are presented for all species examined, along with distributional notes and type information.

INTRODUCTION

The long-horned caddisflies, making up the family Leptoceridae and including nearly 900 described species, have been of special interest to caddisfly systematists, freshwater biologists, and naturalists for many years because of their worldwide distribution, the broad range of ecological tolerances of various species, the large size and colorful appearance of several common members, and the very diverse morphological characteristics exhibited in the different species groups.

Two subfamilies are currently recognized in the family: Leptocerinae Leach, 1815, and Triplectidinae Ulmer, 1906. A large number of species described in Leptocerinae have been assigned to the genus *Athripsodes* Billberg, 1820 (*Leptocerus auctt. nec* Leach; see Milne, 1934, and Kimmins,

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1949). As pointed out by Morse and Wallace (1975), the genus Ceraclea Stephens, 1829, which has been considered a synonym of Athripsodes for nearly 100 years, should actually be recognized as distinct from it because of many physical and behavioral differences in the larval, pupal, and adult stages of these two evolutionary lineages. The two genera thus compose a separate tribe of Leptocerinae: Athripsodini Billberg.

MATERIAL STUDIED

Specimens Examined

In the course of the study, it was necessary to examine a considerable number of type and nontype specimens deposited in European and North American collections. Persons and institutions who helped make these examinations possible are listed in the acknowledgments. The genus Ceraclea includes 89 currently recognized species, of which 27 of the 30 species in the subgenus Ceraclea and 38 of the 48 species in the subgenus Athripsodina were available for study. Good illustrations of the inaccesible 13 species may be found in the literature cited in the synopsis of species. A detailed study of the 11 species in the African subgenus Pseudoleptocerus will appear at a later date.

Whenever possible, types were examined to assure the correct association of names and species. Repositories of the types include the following institutions and personal collections, listed alphabetically according to city. Asterisks indicate collections whose types were examined in this study.

*Albany, New York, U. S. A., the New York State Museum
*Ann Arbor, Michigan, U. S. A., the University of Michigan insect collection
*Brussels, Belgium, the Royal Institute of Natural Sciences
Budapest, Hungary, the Hungarian Museum of Natural History
Calcutta, India, the Indian Museum
*Cambridge, Massachusetts, U. S. A., the Harvard Museum of Comparative Zoology
Canton, China, the Mell insect collection, the German-Chinese School
The Chinese Science College, Insect Research Institute
Columbus, Ohio, U. S. A., the Ohio State University insect collection
*Geneva, Switzerland, the Geneva Museum of Natural History
Halle, East Germany, the University Zoological Museum
Hamburg, West Germany, the Hamburg Museum
*Leiden, The Netherlands, the National Museum of Natural History
*London, England, the British Museum (Natural History)
*Moraga, California, U. S. A., the D. G. Denning insect collection
Nanking, China, the Nanking Agricultural College Insect Museum
Nara, Japan, the Nara Women's University insect collection
*Ottawa, Ontario, Canada, the F. Schmid insect collection
*St. Paul, Minnesota, U. S. A., the University of Minnesota insect collection
*San Francisco, California, U. S. A., the California Academy of Science
*Stockholm, Sweden, the National Museum of Natural History
*Tallahassee, Florida, U. S. A., the Florida State Collection of

Arthropods at Florida A. & M. University
*Tervuren, Belgium, the Royal Museum of Central Africa
*Urbana, Illinois, U. S. A., the Illinois Natural History Survey
Warsaw, Poland, the Zoological Institute of the Polish Academy of Science
*Washington, District of Columbia, U. S. A., the United States National Museum
*Zaragosa, Spain, the L. Navás insect collection, the College of the Savior boys' school

Checklist of Species

The classification of Ceraclea, including subgenera, species groups, and recognized species, is given below as a convenience in following and orienting the sections which follow.

Genus Ceraclea Stephens, 1829

Subgenus Ceraclea Stephens, 1829

Fulva Group

cama (Flint), 1965. N. Carolina, N. Amer. Fig. 33.
vertreesi (Denning), 1966. Oregon, N. Amer. Fig. 34.
biwaensis (Tsuda and Kuwayama), 1950. Japan. Fig. 35.
resurgens (Walker), 1852. N. transcontinental N. Amer. Figs. 36, 36'.
alces (Ross), 1941. N. centr. N. Amer. Fig. 37.
alboguttata (Hagen), 1860. Europe. Fig. 38.
transversa (Hagen), 1861. Centr. and NE. N. Amer. Figs. 22, 39.
latahensis (Smith), 1962. W. N. Amer. Fig. 40.
fulva (Rambur), 1842. W. Palearctic Region. Figs. 6, 41.
albimacula (Rambur), 1842. Europe. Fig. 42.

Submacula Group

submacula (Walker), 1852. Great Lakes region, N. Amer. Fig. 43.

Senilis Group

punctata (Banks), 1894. Centr. and NE. N. Amer. Fig. 44.
uvalo (Ross), 1938b. Centr. E. N. Amer. Fig. 45.
maculata (Banks), 1899. Centr. and E. N. Amer. Figs. 17, 46.
spongillovorax (Resh), 1974. Illinois, N. Amer.
senilis (Burmeister), 1839. W. Palearctic Region. Fig. 47.
cancellata (Betten), 1934. Centr. and E. N. Amer. Figs. 20, 48.

Nigronervosa Group

erulla (Ross), 1938b. Ohio, N. Amer. Fig. 49.
copha (Ross), 1938a. Wyoming, N. Amer. Fig. 50.
ramburi Morse, new species. Centr. Europe. Fig. 51.

nigronervosa (Retzius), 1783. Transcontinental Palearctic Region and Alaska, N. Amer. Fig. 52.
erratica (Milne), 1936. Great Lakes region, N. Amer. Fig. 53.
albosticta (Hagen), 1861. Great Lakes region, N. Amer. Fig. 54.
mentiea (Walker), 1852. N. centr. and NE. N. Amer. Fig. 55.
slossonae (Banks), 1938. Centr. and SE. N. Amer. Fig. 56.
ophioderus (Ross), 1938a. Centr. and SE. N. Amer. Fig. 57.

Unplaced Species of Ceraclea (Ceraclea)

distinguenda (Martynov), 1936. Rewa, India. Fig. 58.
floridana (Banks), 1903. Florida, N. Amer.
nygmatica (Navás), 1917a. E. Turkey.
superba (Tsuda), 1942b. Japan. Fig. 59.

Subgenus Pseudoleptocerus Ulmer, 1907a

minima (Kimmins), 1956. Sierra Leone, Afr. Fig. 60.
aurifera (Navás), 1931. Zaire, Afr.
chirindensis (Kimmins), 1956. Mozambique, Afr.
congolensis (Mosely), 1939b. Zaire, Afr.
corbeti (Kimmins), 1957. Uganda and Ethiopia, Afr. Fig. 62.
cuprea (Barnard), 1934. Centr. and southern Afr.
njalaensis (Mosely), 1933. Sierra Leone, Afr.
pulchra (Ulmer), 1912. The Cameroons, Afr.
quadrispina (Marlier), 1965. Angola, Afr.
schoutedeni (Navás), 1930. Centr. Afr. Fig. 61.
squamosa (Ulmer), 1905. Centr. Afr.

Subgenus Athripsodina Kimmins, 1963

Spinosa Group

microbatia (Marlier), 1956. L. Tanganyika, Afr. Fig. 63.
batia (Mosely), 1939b. Zaire, Afr. Fig. 64.
spinosa (Navás), 1930. Kalémié, Zaire, Afr. Fig. 65.

Tarsipunctata Group

brevis (Etnier), 1968. Minnesota, N. Amer. Fig. 66.
alagma (Ross), 1938a. N. centr. and NE. N. Amer. Fig. 67.
tarsipunctata (Vorhies), 1909. Centr. and E. N. Amer. Figs. 15, 19, 24, 27, 68.
nepha (Ross), 1944. Centr. N. Amer. Fig. 69.
protonepha Morse and Ross, new species. SE. N. Amer. Fig. 70.

Arielles Group

arielles (Denning), 1942. N. centr. N. Amer. Fig. 71.

Dissimilis Group

wetzeli (Ross), 1941. NE. N. Amer. Fig. 72.
miyakonis (Tsuda), 1942b. Japan. Fig. 73.
sobradieli (Navás), 1917b. Pyrenees, Europe. Fig. 74.
dissimilis (Stephens), 1836. Europe. Figs. 18, 75.
indistincta (Forsslund), 1935. Szechwan, China. Fig. 76.
lobulata (Martynov), 1935. Amur region, Siberia. Fig. 77.

Diluta Group

diluta (Hagen), 1861. N. centr. and E. N. Amer. Fig. 78.
perplexa (MacLachlan), 1877. N. Europe. Fig. 79.

Annulicornis Group

aurea (Pictet), 1834. Centr. Europe. Fig. 80.
sibirica (Ulmer), 1906. Amur region and Korea. Fig. 81.
hastata (Botosaneanu), 1970. Korea. Fig. 82.
excisa (Morton), 1904. N. Palearctic Region and NW. N. Amer. Figs. 3, 5, 10, 11, 83.
annulicornis (Stephens), 1836. Holarctic Region. Figs. 8, 13, 84.
ruthae (Flint), 1965. NE. N. Amer. Fig. 85.
bicalcarata (Schmid), 1970a. Mongolia. Fig. 86.
shuotsuensis (Tsuda), 1942a. Korea. Fig. 87.

Riparia Group

riparia (Albarda), 1874. Centr. Europe. Fig. 88.
yangi (Mosely), 1942. Foochow, China. Fig. 89.
modesta (Banks), 1920. Borneo. Fig. 90.
isurumuniya (Schmid), 1958. Ceylon. Fig. 91.
forcipata (Forsslund), 1935. Szechwan, China. Fig. 92.
flava (Banks), 1904. Centr. and E. N. Amer. Fig. 93.
kamonis (Tsuda), 1942b. Japan. Fig. 94.
ancylus (Vorhies), 1909. Centr. and E. N. Amer. Fig. 95.
neffi (Resh), 1974. Kentucky and Virginia, N. Amer.
nankingensis (Hwang), 1957. Nanking, China. Fig. 96.

Marginata Group

fooensis (Mosely), 1942. Foochow, China. Fig. 97.
martynovi (Forsslund), 1940. Rewa, India, and Ceylon. Fig. 98.
marginata (Banks), 1911. Bengal, India. Fig. 99.

Unplaced Species of Ceraclea (Athripsodina)

dingwuschanella (Ulmer), 1932. SE. China. Fig. 100.
ensifera (Martynov), 1935. Amur region, Siberia. Fig. 101.
kashingensis (Tsuda), 1943. Centr. China. Fig. 102.
kolthoffi (Ulmer), 1932. SE. China. Fig. 103.
major (Hwang), 1957. Kwangsi, China. Fig. 104.

mitis (Tsuda), 1942b. Japan. Fig. 105.
norfolki (Navás), 1917c. Spain.
signaticornis (Ulmer), 1926. Kwangtung, China. Fig. 106.
ungulifera (Kimmins), 1963. NE. Burma. Fig. 107.
variabilis (Martynov), 1935. Amur region, Siberia. Fig. 108.

MORPHOLOGY

Numerous writings have proven useful in developing an understanding of the morphology of caddisflies and the Leptoceridae in general and of the Athripsodini and Ceraclea in particular. Significant contributions to the study of the morphology of the immature stages of Leptoceridae have been made by Klapálek (1888), Thienemann (1905), (Silfvenius) Siltala (1905, 1906, 1907), Vorhies (1909), Lloyd (1921), Lestage (1921), Ulmer (1955), Marlier (1962), Lepneva (1966), and Hickin (1967). Especially useful discussions of adult leptocerid morphology include those of MacLachlan (1877), Ulmer (1907a, 1909, 1912, 1951), Martynov (1924), Barnard (1934), Betten (1934), Mosely (1939a), Mosely and Kimmins (1953), and Marlier (1962). Matsuda (1965) has summarized studies of the insect head and Crichton (1957) has examined the mouthparts of adult caddisflies in detail. The general homologies of male insect genitalia have been discussed by Snodgrass (1935, 1957), Michener (1944), Gustafson (1950), Nielsen (1957a), and Matsuda (1958) and the homologies of male caddisfly genitalia have been compared by Zander (1901), Ross (1944, 1956), Nielsen (1957b, 1970), and Schmid (1970b).

As suggested by Snodgrass (1960), the term sulcus is used below to indicate grooves of purely functional origin. The term suture is reserved for grooves marking lines of fusion of formerly distinct plates. The terms sulcus and suture should not be confused with membranous lines in which sclerotization has been lost.

Larva

The larvae of this family are difficult to associate with the adults by the so-called "metamorphotype method" (Milne, 1938) because the newly pupating insect pushes the old larval exuviae out the rear of its case. A technique to induce egg-laying has been discovered by Resh (1972) which permits association of identified females with subsequently reared larvae.

Fully grown leptocerid larvae are usually small, between 5 and 14 mm. long, and strikingly slender (Brindle, 1962). Most species have an oblong head (Fig. 1). Ordinarily the antennae are quite long, at least eight times as long as wide (Ross, 1944), are usually situated behind the bases of the mandibles, and have a distal seta (Fig. 1A). The gular sclerite is of various shapes, often classed as either longitudinal-rectangular (Fig. 1B), triangular (Fig. 2B), or tapezoid/barrel-shaped (Fig. 3B). In addition to the Y-shaped ecdysial line, a pair of subocular lines often extend to the hind margin of the head (Fig. 3C). The mesonotum is not as strongly sclerotized as the pronotum and, like the latter, is separated into a pair of plates by a longitudinal mesal membranous line (Figs. 4, 5). The femora are apparently divided into two segments. In most genera the abdominal gills consist of individual filaments when they are present at all. The case is ordinarily a long, gradually tapering cone made of sand grains (Fig. 7) or plant material.

An extensive account of the structure of Athripsodini larvae may be found in the work of Lepneva (1966). Features of particular interest include the development of a pair of peculiar, longitudinal, dark, oblique or bracket-shaped bars on the posterior angles of the mesonotum (Figs. 4, 5) and the presence of tufts of abdominal gill filaments. The mesonotal bars are a derived condition for the tribe since they are not known elsewhere in the order. The multifilamentous gills are similar to those seen in the sister family Calamoceratidae and therefore probably were present in the hypothetical ancestor of the leptocerids.

Within Athripsodes the dark mesonotal bars are oblique and straight (Fig. 4), the head is oblong (Fig. 2), and the gula is narrow and triangular (Fig. 2B). The case is a typical elongate, tapering tube made of sand grains (Fig. 7).

The larvae of Ceraclea species, on the other hand, each have bracket-shaped mesonotal bars (Fig. 5), a broad head (Figs. 3A, 3B), and a trapezoid or barrel-shaped gula (Fig. 3B). Most larvae of this genus have a pair of parafrontal areas, each of which is delineated by a light line paralleling the lateral arms of the ecdysial line (Fig. 3A). These lines are absent in all other Leptoceridae and in the subgenus Pseudoleptocerus (Corbet, 1958). These areas are poorly defined posteriorly in the Ceraclea (C.) Fulva Group (Fig. 6). The case of Ceraclea species larvae is usually of a cornucopia shape (Fig. 8), although numerous modifications occur. It is highly likely that all of these conditions are derived character states for the genus Ceraclea since they do not occur elsewhere in the family.

Additional characters useful for separating the species of Athripsodes and Ceraclea in the immature stages can be found in the discussion by Morse and Wallace (1975).

Pupa

Of special interest in the morphology of leptocerid pupae are the long antennae which are coiled around the abdomen (Fig. 9); the simple, elongate, serrate mandibles (Fig. 10); and the spinulose tubercles on the posterior angles of the first abdominal segment (Fig. 11).

The characteristics of the Athripsodini pupae have been discussed by Lepneva (1966). As in the larvae, the gills occur in tufts and the body and case are narrowed posteriorly.

Lepneva (1966) distinguished pupae of species of Athripsodes from those of Ceraclea species by the reduced number of abdominal gills (on segments 1-3 or 2-3 as opposed to 2-8 or 2-7 in Ceraclea), the straighter anal rods (Figs. 12, 13), and the round or vertical, slit-like opening of the pupal case. This opening is horizontal in Ceraclea.

Adult Head and Thorax

The Leptoceridae are unusual among caddisflies in that the males are generally larger and with more distinct color markings than the females of the same species. The antennae are very long (Fig. 14), usually longer in males than in females, with bulbous scapes rarely longer than the head. The five segments of each maxillary palp are relatively long, thin, densely hairy, and with a mottled loss of sclerotization in the apical segment best seen in specimens preserved in alcohol (Figs. 23, 24). The ocelli are absent. In

many species the vertex is marked by three sulci (Fig. 21): a midcranial sulcus (Matsuda, 1965) and a pair of lateral sulci (Ross, 1944). Usually the midcranial sulcus is divided anteriorly into a pair of frontal sulci (Snodgrass, 1935) which pass between the antennal bases and sometimes extend to the anterior tentorial pits. The frontal sulci are very close to each other between the antennae such that they define a dorsal diamond-shaped area referred to by Ross (1944) as the "dorsal triangle." The lateral sulci are strongest posteriorly and are incomplete or joined to the dorsal triangle or to the dorsolateral portion of the antennal sulci anteriorly. The anterior portion of the of the vertex bears two pairs of warts, one pair of which is located in the dorsal triangle and the other lies outside it along its posterio-lateral edges. A third pair of warts is situated posteriorly between the lateral sulci and the eyes. Various combinations of these warts and sulci may be absent or indistinct in different species groups. The fact that they are all present in members of both leptocerid subfamilies indicates that they were probably present in the ancestor of the family.

Throughout the Leptoceridae the middle of the pronotum is deeply concave and the rounded anterior margin of the mesonotum projects strongly over and above its two lateral lobes (Fig. 15). Setae occur in a pair of long, irregular lines on the mesonotum and two small clusters on the short mesoscutellum. The katepisterna on the meso- and metathoracic segments are each truncate by a short transverse sulcus (Fig. 17) or constricted without the sulcus (Fig. 16). The mesofurca is large and with a long anterior projection (Ross, 1967).

The legs are long, slender, and hairy. Movable spurs are arranged on the tibiae of the three legs in combinations of 0, 1, 1 or 0, 2, 2 or 1, 2, 2 or 2, 2, 2 or 2, 2, 4. Presumably the latter arrangement is the ancestral character state in the family as is evidenced by the larger number of spurs in related families. In addition to the spurs, each tarsal segment bears a pair of apical spines and the middle tibiae and the middle and hind tarsi each bear a double row of spines.

Wings

The forewings (Figs. 27A, 28A) are typically long and narrow, no doubt associated with the strong rapid flight of these insects, while the hindwings (Figs. 27B, 28B) are slightly shorter and more pliable. The latter are broad in the Triplectidinae and in many species of Athripsodini, Nectopsyche, and Parasetodes. The wing venation is not strongly divergent from the ancestral caddisfly condition (Ross, 1956), but does have a few interesting modifications. The venational terminology used here is consistent with the interpretation of Hamilton (1972).

Veins Sc and R are usually rather straight, terminating in the costal margin before the apex. A crossvein sometimes unites the two just before their termination and occasionally a crossvein is present between R and the anterior branch of S. A so-called "stigma" is often evident in cell Sc between the points of termination of Sc and R.

Cell S_1 is variously present or absent in both wings, apparently having been lost independently in different leptocerid lineages. Contrary to the opinion of most earlier workers (MacLachlan, 1877; Ulmer, 1907a; Martynov, 1924; Barnard, 1934; Mosely, 1939a; Mosely and Kimmins, 1953; and Marlier, 1962), cell S_3 (fork 2 of authors) is present in both wings in Leptoceridae as is evidenced by the position of the conspicuous corneus point (nigma) in that

cell (Betten, 1934). On this basis, vein S_4 is fused with the anterior branch of media (MA) for much of its length. Cell S_2 ("discal cell"), set off by a sectoral crossvein (s), is present (closed) in the hindwings of Triplectidinae and absent in those of Leptocerinae. In most species of the subgenus Pseudoleptocerus and in the genera Leptocerus and Setodes, the usual first fork of S in the hindwing branches beyond the origin of cell S_3 (Fig. 28B), leaving a wide space between R and the stem of S.

Most species have only two branches of M, with cells M_1 and M_3 (forks 3 and 4 of authors) being absent. The females of Triplectidinae, Leptorussa, and of most species of Athripsodini have an additional branch of M in the forewing (Fig. 28A). Most authors consider it to be a separate M_2 (fork 3 present), but it could be M_{1+2} (MA) as well. This additional branch of M is present in the hindwings of both sexes of Triplectidinae species. A median crossvein (m), delineating a cell M_2 ("median cell") is never present in Leptoceridae. Because Cu branches from M and is joined to it by m-cu nearer the apex of the forewing, it is sometimes possible to mistake the so delineated "thyridial cell" for a true median cell. Crossvein m-cu is always absent in the hindwings of leptocerids. An apparent posterior branch of media (MP) is often evident close to the stem of Cu in the hindwings of Leptoceridae. This "false vein" seems to be an artifact of the convoluted wing membrane.

Cell Cu_1 (fork 5) is always present in the forewings of long-horned caddisflies but has been lost in the hindwings of species of Triaenodes, Adicella, and Erotesis. The plical vein (P) terminates in the forewing margin at the level of cu-p along with fused E + 1A + 2A, forming a small vein bulla sometimes called the "arculus." On the other hand, these veins end at the hindwing margin independently.

The irregular transverse line formed by veins and crossveins about two-thirds the distance from the base (including s, S_4 base, m-cu, Cu_2 base, cu-p, and arculus, respectively from anterior to posterior in the forewing) is sometimes referred to as the "line of anastomosis" or "cord."

Genitalia

Excellent overviews of homologies and terminology of male genitalia of caddisflies can be seen in the works cited in the introduction to this section. In addition, Nielsen (1970) has reviewed current thinking on homologies of external and sclerotized internal female genitalic parts and Unzicker (1968) has compared their internal membranous structures.

The abdomen of a typical leptocerid consists of independent tergal and sternal plates on segments 1 through 8. The sternum of the first segment is narrow and closely applied to the metacoxae. Dark antecostal sutures are evident along the anterior and anterio-lateral margins of the sternites and tergites (Fig. 29A). Many Leptocerinae bear an additional pair of longitudinal, dorso-lateral sulci to about one-third the distance from the anterior margin. A pair of tiny rugous sclerites usually occur in the intersegmental membranes between the fifth and sixth tergites.

The ninth segment of the male is typically synsclerotized (Fig. 29). A short, punctate, semimembranous acrotergite is often present, though sometimes reduced or divided in the middle. A circumferential antecosta is usually evident, but often narrowed. In many species of Leptocerinae a pair of sclerotized strips extend from the posterior lateral margins of the segment into the genital chamber and articulate or fuse with a corresponding pair of

strips from the sclerotic "phallic shield" surrounding the phallobase (see discussion of phallus below). They were described by Schmid (1968) as "assez larges lames chitineuses" and as "larges bandes externes" and were considered by him to be the principle generic characteristic of Poecilopsyche.

In most species of the family, the tenth tergite is connected with the ninth by a narrow strap extending below the superior appendages. It may be fused to the ninth tergite dorsally in addition to, or in place of, the lateral connections. In most species of Triplectidinae and in Ceraclea, the tenth tergite is basically a single piece, although often with smaller lateral lobes or processes. In a large number of genera, however, it is deeply divided down the middle (Fig. 30). Nielsen's (1957b) discussion of Athripsodes cinereus (as Leptocerus) in comparison with species in related families indicates that the divided condition was probably the ancestral character state in the forerunner of the Leptoceridae. The fused apex of the tenth tergum of most species of Triplectidinae and Ceraclea has several hair sensilla. Species in the subgenera Ceraclea and Pseudoleptocerus have a separate sclerite, here referred to as the "subanal plate," suspended in the membranes below the anus (Fig. 29C; indicated by broken lines beneath the tenth tergum in Figs. 29A and 29B).

Between the ninth and tenth tergites is a pair of superior appendages (called "cerci" by several North American workers). Nielsen (1970) argues that these processes are not cerci, evidently because they are apparently in the "wrong" place. However, his observation (1957b) that an eleventh segment is present in Rhyacophila, Tinodes, and Polycentropodidae below the tenth tergite tends to indicate the direction of migration of the cerci through the membranes along the ventro-lateral margins of the tenth tergite to their present position. Admittedly it is also possible that a caddisfly ancestor was a homeotic mutant that gained an extra pair of cerci between the ninth and tenth tergites and then lost its true cerci or, it is possible that the cerci were first lost in this hypothetical ancestor and another pair of very similar structures arose subsequently in between the ninth and tenth tergites. However, the hypothesis of the migration of the cerci seems to require fewer assumptions and is compatible with Nielsen's observed position of the vestigial eleventh segment structures. Until careful studies of embryology and musculature can be made, though, it seems best to retain the general term. The superior appendages may be very long or quite short and are sometimes fused with the ninth or tenth tergites and are not at all evident except as indicated by a pair of clusters of setae. In Ceraclea they are often fused with each other and with the ninth tergum basally.

The homologies of the inferior appendages and of the phallus have long been a subject of debate. Snodgrass (1957) and Matsuda (1958) concluded that they are of independent origin, but Michener (1944) and Nielsen (1957a) are of the opinion that they are modified ninth segmental limb appendages. Resolution of this argument will require much phylogenetic study of pupal development and musculature. The inferior appendages (variously "parameres" or "claspers" or "gonopods" or "gonapophyses") assume a wide range of shapes in the Leptoceridae. In their simplest form (Figs. 29A, 29C) they each consist of a relatively large coxopodite and a smaller apical segment or harpago. The coxopodite may bear any of several modifications, the most common of which include (a) a subapico-dorsal, semimembranous or sclerotized projection, usually with scattered, long setae, (b) an immovable sclerotized projection of the ventro-basal portion of the segment, commonly with stout apical or subapical spines, (c) an articulated, only moderately sclerotized lobe with

scattered long setae which arises in the ventral meso-basal region of the segment in many species of Triplectidinae (not shown in Fig. 29), (d) a longitudinal, mesal ridge often bearing short, stout setae, and (e) a rounded or pointed, glabrous posterior projection of the dorsal subanterio-mesal margin which, together with the process of the opposing coxopodite, form a pair of "phallic guides" in many species. The mesal bases of the two coxopodites are usually somewhat elongate anteriorly, flattened on the meson, and fused to some extent with each other, with the ventral margin thin and the dorsal margin broadened laterally into a "basal plate" (Nielsen, 1957b, 1970) in the otherwise membranous genital chamber. The harpago is generally darker than the coxopodite and curved mesad, often with a few short setae.

Ross (1956), Nielsen (1957b, 1970), and Schmid (1970) all agree that the ancestral caddisfly probably had the following phallic structures (Fig. 31): (a) distal endophallic membranes bearing the gonopore opening of the ejaculatory duct, (b) a subapical sclerotized phalicata (Ross, 1956; a term preferred over "aedeagus" since the latter is commonly used as a synonym for the entire phallus), (c) an antepenultimate, membranous endothecal portion bearing a pair of lateral parameres, and (d) a proximal sclerotized phallobase. Nielsen (1957b) recognized also (e) a "phallotremal sclerite" at the endophallic gonopore opening in the superfamily Limnephiloidea, generally U-shaped in Leptoceridae in dorsal view, (f) an anterior "phallic apodeme" inside the body wall which extends to, and surrounds, the phallic foramen through which the ejaculatory duct passes from the haemocoele, and (g) a sclerotized rim in the phallocrypt membranes at their junction with the phallobase. The latter structure is referred to here as the "phallic shield." It appears to be a common feature in caddisflies from which various sclerotized strips and periphallic processes may be produced. These strips and processes actually constitute two separate classes of projections of the phallic shield. Strips are sclerotized productions of the phallic shield which continue in the same plane as the genital chamber membranes. Periphallic processes are external projections outside the plane of the phallic shield and its adjoining genital chamber membranes. Examples of phallic shield strips include the "tergal strap" of Ross and Schmid or the "unpaired sclerotic stripe of the paraprocts" of Nielsen in Rhyacophila, the "internal sclerite" of Nielsen in Agapetus fuscipes, the "sclerite connecting the proximal end of the phallus with the sclerite of the genital chamber" of Nielsen in Tinodes waeneri, the "rod-like extension of the sclerite of the phallocrypt" of Nielsen in Silo nigricornis and Stenophylax stellatus. Examples of external periphallic processes include the "clasper hangers" of Ross or the "horns" of Nielsen or the "tenons" of Schmid in Rhyacophila and the "swan's neck processes" in Nectopsyche (Ross, 1944, as Leptocella). Either class of apophyses may fuse or articulate with other corresponding apophyses from adjoining organs or they may merely terminate without apparent associations with nonphallic structures.

In most species of Leptocerinae a pair of lateral strips have developed from the phallic shield which articulate or fuse with the corresponding pair of strips from the posterior lateral margins of the ninth sternum, forming a pair of bands above the bases of the coxopodites (Fig. 29; see discussion of ninth segment above). For the sake of clarity, these have been omitted from Figs. 33-108, and among these, the phallic shield has been illustrated in only Figs. 48D, 63D, 64D, and 65A.

In the Athripsodini, an additional pair of phallic parameres ("dorsal parameres") developed above the phalicata from the endothecal membranes.

A thorough comparative analysis of female genitalia is not attempted here. Generally, however, the ninth sternum of female leptocerids consists of one, two, or three plates arranged symmetrically on a longitudinal axis (Figs. 19, 18, and 20, respectively). The ninth tergal plate is usually undivided and often fused with the anterior lateral margins of the sternal plate(s) (Figs. 18A, 18B, 18C). The tenth tergite is fused with that of the ninth usually along with the superior appendages (Figs. 18A, 18B). A pair of large, vertical, sclerotized lamellae, generally with thickened, setose anterio-ventral margins, flank the genital and anal openings. The internal bursal sclerite (Fig. 18D; "bursa copulatrix" of Ross, 1944) often assumes characteristic shapes in the different species.

Many of the females of North American and British species of Athripsodini can be distinguished by using the works of Ross (1944) and Kimmins (1964). In species of the genus Ceraclea a pair of small rounded sclerites have developed at the posterior apico-lateral angles of the ninth sternites (Fig. 18D, rs). They have apparently been lost in the subgenus Ceraclea, but are especially well-developed in the Tarsipunctata Group (Fig. 19) and in several other species of the subgenus Athripsodina. In one line of the subgenus Ceraclea, a pair of grooves has developed above the lateral margins of the ninth sternum (Fig. 20) and most members of this lineage have also developed a third, mesal sternal plate between the two lateral sclerites.

PHYLOGENETIC METHOD

An integral part of this study is the desire to provide a logically sound conceptual framework for the genus Ceraclea which will be useful to as wide a variety of biologists as possible, including not only systematists but ecologists, physiologists, geneticists, cytologists, zoogeographers, behaviorists, and so forth. This framework can be developed best by assessing the relationships of known species in the genus through carefully reconstructing its phylogenetic history and by graphically depicting the inferred sequence of evolutionary events in a phylogenetic tree. Recent clarification of the logic of phylogenetic systematics, notably in the works of Hennig (1950, 1965, 1966), Schlee (1968), Hull (1970), Nelson (1970), Brundin (1972), Ross (1974), and many others, has provided a rational background for making phylogenetic inferences and constructing phylogenetic trees.

No fossils of the genus Ceraclea are known. Consequently, the determination of ancestral and derived character states was achieved by ex-group comparisons (as opposed to in-group comparisons, Ross, 1974). Species of Ceraclea were first assembled in small groups according to their common possession of particular character states. These character states were then compared with those of other groups within and outside the genus. Unique character states were considered derived for the group; character states similar to those in other groups were considered ancestral. Groups which had been assembled on the basis of ancestral character states were dissolved and their species examined for other character states suggesting different group assignments. This procedure continued until thirteen monophyletic groups were finally recognized, each of which had developed one or more derived character states (Fig. 32, Ceraclea).

These groups were then subdivided into complexes and the groups themselves were assembled into larger clusters on the bases of similar ex-group

comparisons. Consistent use of this method of inference through successive levels of grouping resulted in a hypothetical reconstruction of the evolutionary sequence of divergences in the genus. Each point of divergence of sister groups is considered a point in the evolution of the parent line for which a hypothetical ancestor can be defined according to the character states in common to the sister groups. The ancestors and the character changes which took place along each daughter lineage are discussed in the following section. The sequence of inferences for Ceraclea, its ancestors, subgenera, and species groups is graphically portrayed in Fig. 32. The details of the evolution within the species groups will appear at a later date.

This method of phylogenetic study does not produce a static conceptual scheme, but rather one which may change with the discovery of additional derived character states and one which readily accommodates new discoveries of fossil and contemporary species. Occasionally two sets of character states may lead to conflicting inferences, in which case one character state must be assumed to have evolved independently two times. Each time this problem arose in this study, the species were examined for other character states which might lend the weight of evidence for one probable evolutionary sequence over the other. In cases where additional character states were not found, the less complex, differently formed, or lost character states were assumed to have had a higher probability of evolving independently than the complex, similarly formed, or gained character states.

Thus the recognition of unexamined character states may reinforce earlier inferences or may lead to new inferences. Obviously the phylogenetic scheme based on the most kinds of characters in the most ontogenetic stages has the highest probability of being the correct historical reconstruction and therefore has the greatest potential for use by other biologists.

EVOLUTIONARY HISTORY AND RELATIONSHIPS

Pre-Ceraclean Ancestors

The evolution of the families of Trichoptera has been discussed by Ross (1967). In this scheme, the family Leptoceridae is a highly evolved line of the leptocerid branch of the Limnephiloidea. Its sister group is the family Calamoceratidae.

Using the rational inducto-deductive scheme and methods outlined in the preceding section, it is inferred from the material in the chapter on morphology that the hypothetical ancestor of Leptoceridae (Fig. 32) probably had a slender larva with an oblong head and relatively long antennae (Fig. 1). The gular sclerite was longitudinal-rectangular. The mesothorax was not unusually marked and the notum was divided into a pair of plates by a mesal, longitudinal membranous line (Fig. 4). Multifilamentous gills occurred in three rows along the abdomen on segments 1-8. It made a long, gradually tapering case of sand and salivary secretions (Fig. 7). The pupa had long anal rods (Figs. 9, 12, 13) and a circular opening to its case.

The adult had long antennae (Fig. 14), three pairs of head warts behind the antennae (Fig. 21), a pair of lateral sulci and a midcranial sulcus. The maxillary palps were long, hairy, five-segmented, and with the apical segment "flexible" due to a mottled loss of sclerotization (Fig. 23). The pronotum had become very concave in the middle and the rounded anterior margin

of the mesonotum projected over it (Fig. 15). The setae on the mesonotum had become scattered in a pair of irregular lines and a short sulcus truncated the dorsal margin of the katepisterna of the meso- and metathoracic segments (Fig. 17). The legs were long and slender with tibial spurs arranged in a sequence of 2, 2, 4 on the three pairs of legs.

The forewings were much narrower than those of the predecessors of this species. S_4 and M_{1+2} in each wing had become fused for much of their length (Figs. 27, 28). The males had only one distinct branch of media in the forewing (Fig. 27A) and the females had two (Fig. 28A). The median crossvein had been lost in both front and hind wings and sectoral crossvein was still present in both wings.

The ninth abdominal segment was annular, without posterio-lateral sclerotized strips projecting into the genital chamber. The tenth segment was probably divided longitudinally (Fig. 30) and attached to the ninth segment only by a pair of straps below the superior appendages. The superior appendages were not fused with either the ninth or tenth tergites or with each other (Figs. 29, 30). The inferior appendages had each developed a characteristic semimembranous subapico-dorsal lobe with scattered long setae and had each retained a large harpago (Figs. 29A, 29C). The phallus (Fig. 31) had a cylindrical phallobase, a narrow phallic shield without lateral sclerotized strips, a single pair of parameres, a tubular phalicata and a U-shaped phallotremal sclerite. This leptocerid ancestor gave rise to two sister species, the ancestors of Triplectidinae and Leptocerinae.

The Triplectidinae ancestor lost its phallic parameres and its phalicata became reduced to a peculiar V-shaped cap at the apico-dorsal end of a much-elongated phallobase.

The Leptocerinae progenitor lost the sectoral crossvein in each hindwing (discal cell opened) and lost one of the two distinct branches of M in the hindwing (Fig. 27B). This ancestor produced the subsequently highly modified species Leptorussa darlingtoni (Banks) and Ancestor 1.

Ancestor 1 developed a distinctive set of two pairs of articulating sclerotized strips; one pair from the posterio-lateral margins of the ninth segment and one pair from the phallic shield, forming a sclerotized band above the bases of the inferior appendages (Fig. 29). This species gave rise to the precursor of Athripsodini on the one hand and to the progenitor of the rest of the Leptocerinae on the other.

In the ancestor of the higher leptocerine genera, the extra branch of M in the female forewing was lost, the harpago became reduced, one of the apical spurs of the foretibia was lost, and the larval gills became unifilamentous.

The Athripsodini progenitor acquired a second dorsal pair of phallic parameres which lay close against the top of the tubular phalicata (Figs. 31, 60D). Its larva developed a pair of dark mesonotal bars (Figs. 4, 5) and the larval gula became narrow posteriorly (Fig. 2B). Two principle lineages, leading to Athripsodes and Ceraclea, developed from this hypothetical species.

In the progenitor of Athripsodes, the subapico-dorsal process of the coxopodite became heavily sclerotized (Fig. 26) and then became reduced in size (Fig. 25). Its larva and pupa lost the gills on abdominal segments 4-8.

In the ancestor of Ceraclea, the midcranial sulcus in the adult head was lost (Fig. 22) and the apex of the fourth maxillary palp segment became flexible due to a mottled loss of sclerotization (Fig. 24). It developed parafrontal regions on the head of the larva (Fig. 3), the larval head became rather broad in relation to its length (Figs. 3, 6), and the gular sclerite became further

reduced posteriorly and expanded anteriorly such that it appeared longer transversely than longitudinally (Fig. 3B). The dark mesonotal bars became longer and bent about in the middle, a shape especially evident in the final instar of Recent species (Fig. 5). The two halves of the tenth tergum in the male genitalia fused on the meson (Fig. 29B). This ancestor also developed the exceedingly rare capacity to ingest whole particles of freshwater sponge, including the spicules (Resh, Morse, and Wallace, 1975).

Evolution within the Genus Ceraclea

Two lineages arose from this generic progenitor, the forbearer of the subgenus Athripsodina and Ancestor 2.

In Ancestor 2, the ventral apex of the phallobase became very long, serving as a sort of accessory phallic guide for the cylindrical phalicata (Fig. 49D). A unique subanal plate developed in the external membranes beneath the anus under the tenth tergum (Fig. 29C). The progenitors of the subgenera Pseuoleptocerus and Ceraclea descended from this species.

SUBGENUS Ceraclea. The ancestor of the subgenus Ceraclea lost one of its pairs of phallic parameres and the lateral margins of the phalicata each acquired a longitudinal, rounded groove (Fig. 52D). The descendents of this species included the ancestor of the Fulva Group and the progenitor of the rest of this subgenus.

In the ancestor of the Fulva Group the apex of the tenth tergite became three-pronged, comprising a pair of large lobes with lateral sensilla and a smaller, finger-like lobe between them (Fig. 34E). The mesal ridge of the coxopodite widened considerably and the apex of the harpago achieved a characteristic expansion and supapical triangular projection (Fig. 33C).

The progenitor of the other main line of the subgenus Ceraclea acquired scattered white scales on the forewings of both sexes and the female gained a pair of longitudinal grooves just above the lateral margins of the ninth sternum (Fig. 20). From this species arose the peculiar species submacula and the ancestor of the remainder of the subgenus.

The female of this latter species developed a mesal sclerite on the ninth sternum between the two lateral plates (Fig. 20). It gave rise to the progenitors of the Nigronervosa Group and the Senilis Group.

The forerunner of the Senilis Group had an elongate ventral lobe on the coxopodite (Fig. 44A). In the Nigronervosa Group progenitor, the lateral margins of the tenth tergite developed a pair of ear-like lobes (Fig. 49A).

SUBGENUS Pseudoleptocerus. The ancestor of the subgenus Pseudoleptocerus developed a separate sclerite at the ventro-mesal apex of the ninth sternum of the male. This sclerite was small initially (Fig. 60A, shown in dashed outline), but has undergone remarkable elaboration in later species (Figs. 61A, 61E, 62A, 62E). The 11 species of this lineage are known only from Africa. Many of them have large patches of small, extraordinarily colorful, irridescent scales on the forewings, often with larger white scales appearing along the veins.

SUBGENUS Athripsodina. The ancestor of the subgenus Athripsodina acquired a deep cleft in the ventral apex of the phallobase (Fig. 84E) and a pair of lateral processes separated from the latero-ventral margins of its tenth tergite (Fig. 84A). It produced two lineages leading to the Tarsipunctata-Spinosa Group ancestor and to the ancestor of the rest of the subgenus.

In the Tarsipunctata-Spinosa Group ancestor, the lateral lobes of the tenth

tergite became very long and distinct from the tergite nearly to the base (Fig. 63A). It was the forerunner of an African Spinosa Group ancestor and a North American Tarsipunctata Group ancestor.

The forbearer of the Spinosa Group had very long, slender superior appendages (Fig. 63A), a peculiar anterior elongation of the ventral portion of the phallic shield which fused with the ventral plate of the bases of the coxopodites (Figs. 64D, 65A), a loss of both pairs of phallic parameres (Fig. 64D), and reduced sclerotization of the phalicata. The progenitor of the Tarsipunctata Group acquired a subapical annulation on each phallic paramere (Fig. 66D), the phallobase developed an oblique constriction from about one-third the distance from the anterior end, and the phallic shield became produced at the base of each sclerotized strip into a broadly rounded periphallic projection.

In the ancestor of the rest of this subgenus, most of the sclerotization of the phalicata was lost (Fig. 84E) and the apex of the tenth tergite became upturned (Fig. 71A). It apparently produced three lines: (a) the unusual species arielles in which the apex of the phallobase was highly modified (Figs. 71D-F), (b) the precursor of the Dissimilis Group, and (c) the progenitor of the higher species groups.

In the Dissimilis Group ancestor, the left apex of the phallobase became narrow and downcurved (Fig. 75D). In the ancestor of the remaining four species groups, the left paramere spine moved anteriorly inside a retracted left paramere lobe (Fig. 78D). Three lineages apparently descended from it, also. One led to the Diluta Group forbearer, another gave rise to the precursor of the Annulicornis Group, and the third produced the Riparia-Marginata Group forerunner.

The Diluta Group ancestor lost the lateral processes of its tenth tergite (Fig. 78A) and the phallus became especially short (Fig. 78D). In the Annulicornis Group ancestor, the retracted left paramere spine became reduced (Fig. 80D). In the Riparia-Marginata Group ancestor, the ventral lobe of the inferior appendage became acutely angled with respect to the main body of the coxopodite and greatly increased in size, such that it was nearly as large as the rest of the appendage (Fig. 88A).

Three large spines became differentiated at the apex of the ventral lobe of the coxopodite (Fig. 89C) in the ancestor of the Riparia Group and the phallic paramere spines lined up in a peculiar fashion with the left (anterior) spine bent and its tip inserted into the base of the right (posterior) spine (Fig. 88D). The Marginata Group progenitor underwent a strong reduction of the main body of the inferior appendage, leaving the remaining ventral lobe to perform the necessary clasping functions (Figs. 98A, 98C), the left paramere spine migrated back to a level with the right spine (Fig. 98D), and the lateral lobes of the tenth tergite were lost (Fig. 99A).

FAUNAL SUMMARY

Nearctic Region. The North American fauna of Athripsodini is made up solely of species of the genus Ceraclea, with Athripsodes being confined to the Palearctic, African, and Oriental Regions. Fourteen species of C. (Athripsodina) are Nearctic including all five in the Tarsipunctata Group, arielles, wetzeli in the Dissimilis Group, diluta of the Diluta Group, ruthae and the Holarctic species excisa and annulicornis in the Annulicornis Group, and flava, neffi, and ancylus in the Riparia Group. Twenty-one species of Ceraclea subgenus

occur in North America including six in the Fulva Group, submacula, five in the Senilis Group, eight in the Nigronervosa Group, and floridana.

Palearctic Region. The Palearctic fauna of Athripsodini is composed of nearly as many species of Ceraclea as of Athripsodes. The region appears to be divided in central Asia into West Palearctic and East Palearctic Subregions. Twelve species are in the West Palearctic Subregion, twenty-two are in the East Palearctic Subregion, and three have trans-Palearctic distributions.

The exclusively West Palearctic species of the subgenus Ceraclea comprise fulva, alboguttata, and albimacula of the Fulva Group; senilis; ramburi of the Nigronervosa Group; and nygmatica of the unplaced species of this subgenus. Species of the subgenus Athripsodina inhabiting this subregion include sobradieli and dissimilis of the Dissimilis Group, perplexa of the Diluta Group, aurea of the Annulicornis Group, riparia of the Riparia Group, and norfolki of the unplaced species in this subgenus.

The species of the subgenus Ceraclea living in the East Palearctic Subregion include biwaensis of the Fulva Group and the unplaced species superba. Species of the subgenus Athripsodina in this subregion comprise miyakonis, indistincta, and lobulata of the Dissimilis Group; sibirica, hastata, bicalcarata, and shuotsuensis of the Annulicornis Group; yangi, forcipata, nankingensis, and kamonis of the Riparia Group; fooensis of the Marginata Group; and eight of the ten unplaced species in this subgenus.

The Annulicornis Group species excisa and annulicornis and the Nigronervosa Group species nigronervosa are distributed throughout the northern Palearctic Region.

Oriental Region. Two species of the Marginata Group, martynovi and marginata, and two species of the Riparia Group, modesta and isurumuniya, occur in the Oriental Region as well as the unplaced species ungulifera and distinguenda.

Ethiopian Region. The African continent below the Mediterranean area provides habitation for two groups, the eleven species in the subgenus Pseudoleptocerus and the three species of the Ceraclea (Athripsodina) Spinosa Group.

No Antarctican, Australian, or Neotropical species of Ceraclea are known.

SYSTEMATIC TREATMENT OF Ceraclea SUBGENERA AND SPECIES

Key to Subgenera of Ceraclea (Males Only)

1. Midcranial sulcus present (Fig. 21); fourth maxillary palp segment sclerotized to its apex; tenth tergum strongly divided on the meson, composed of an even number of main pieces (Fig. 30) . . . . . Genus Athripsodes (not treated further).
   Midcranial sulcus absent (Fig. 22); fourth maxillary palp segment flexible apically; tenth tergum fused on the meson, thus having an odd number of main pieces (Figs. 29B, 64B) . Genus Ceraclea, 2
2. Phallobase with a longitudinal cleft of its ventral lip (Fig. 84E) . . . . . Subgenus Athripsodina, in part; key, p. 35.
   Phallobase entire apico-ventrally 3
3. Harpago absent (Fig. 61C); ninth sternum with protracted region well-differentiated, sometimes complex (Figs. 62A, 62E). .

. . . . . Subgenus Pseudoleptocerus (not keyed further), p. 34.
Harpago present; ninth sternum without sclerotized projection 4
4. Phallus with a pair of long, internal spines (Fig. 71D); phalicata inconspicuous; harpago disc-shaped apically (Fig. 71C).
North central N. Amer. . C. (Athripsodina) arielles (Denning), p. 38.
Phallus with spines very short (Fig. 43D) or phalicata and spines large and conspicuous (Fig. 51D); harpago hatchet-shaped apically (Figs. 39C, 43C) or tapered (Fig. 47C) . . . . .
. . . . . Subgenus Ceraclea, key p. 18.

Key to Species of Ceraclea (Ceraclea)*
(Males Only)

1. Apex of tenth tergum divided into two lateral sensilla-bearing lobes and one or two bare mesal fingers (Figs. 36E, 37B).
. . . . . Fulva Group, 2
Apex of tenth tergum entire apically or with a short, simple mesal cleft. 11
2. Ventral margin of phallobase extended in a long, projecting lower lip (Fig. 33D). Eastern N. Amer. . . . . cama (Flint), p. 26.
Ventral margin of phallobase short (Fig. 36D) 3
3. Mesal ridge of coxopodite without a long spine (Fig. 37C) 4
Mesal ridge of coxopodite with a single long spine on its caudal surface (Fig. 41C) 7
4. Superior appendages hardly extending beyond apex of ninth tergum in dorsal view (Fig. 35B). Japan. . . . . .
. . . . . biwaensis (Tsuda and Kuwayama), p. 26.
Superior appendages fused and extending well beyond ninth tergum (Fig. 34B) 5
5. Tenth tergum narrow and broadly concave on ventral margin before the apex in lateral view (Fig. 37A). Northeastern N. Amer.
. . . . . alces (Ross), p. 27.
Tenth tergum broader, upturned from about the middle (Fig. 34A). . . . 6
6. Phallic parameres with apical one-third abruptly narrower, apical two-thirds thin and straight (Fig. 34D); ventral lobe of coxopodite long and acute (Fig. 34A). Western N. Amer.. . . .
. . . . . vertreesi (Denning), p. 26.
Phallic parameres broader, not abruptly narrowed subapically; ventral lobe of coxopodite shorter, especially in western forms, and with two or more stout spines (Fig. 36).
Northern transcontinental N. Amer. . . . resurgens (Walker), p. 27.
7. Spine of mesal ridge of coxopodite extending beyond apex of ridge (Fig. 39C) 8
Spine of mesal ridge of coxopodite much shorter (Fig. 41C) 9
8. Phallic parameres about two-thirds as long as phalicata, each bent slightly and broadened before the apex (Fig. 39D).
Eastern N. Amer. . . . . transversa (Hagen), p. 28.

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*Species not keyed include distinguenda (Fig. 58), Rewa, India; floridana, Florida, N. Amer.; nygmatica, E. Turkey; and superba (Fig. 59), Japan.

Phallic parameres as long as phalicata, gradually curved and of even width to tapered apex (Fig. 40D). Western N. Amer. . . . . latahensis (Smith), p. 28.

9. Ventro-basal lobe of coxopodite long with stout apical spines (Figs. 38A, 38C). Europe. . . . . alboguttata (Hagen), p. 27.
Ventro-basal lobe of coxopodite short, rounded, without spines (Figs. 41A, 41C) 10

10. Tenth tergum only slightly longer than superior appendages and its apico-mesal process bifid (Fig. 41). Europe . fulva (Rambur), p. 28.
Tenth tergum extending well beyond superior appendages and with apico-mesal process short and not strongly bifid (Fig. 42). Europe . . . . . albimacula (Rambur), p. 28.

11. Harpago broadened and hatchet-shaped apically; phalicata inconspicuous; phallic parameres tiny (Fig. 43). Northeastern N. Amer. . . . . submacula (Walker), p. 29.
Harpago tapered; phalicata and usually parameres large and conspicuous (Fig. 47D) 12

12. Tenth tergum with at least one pair of lateral lobes (Fig. 49A) and sometimes with long, stout setae (Figs. 54A, 55A); ventral lobe of coxopodite absent or very broad (Figs. 50, 51) . . . . . .Nigronervosa Group, 17
Tenth tergum without lateral lobes (Fig. 45A); ventral lobe of coxopodite absent (Fig. 48A) or slender (Fig. 44A). Senilis Group, 13

13. Harpago large; latero-ventral edges of tenth tergum deeply excavated in lateral view (Fig. 44A) 14
Harpago slender; latero-ventral edges of tenth tergum only gently concave (Fig. 46A) 15

14. Apex of tenth tergum short, rounded in lateral view (Fig. 44A). Central and eastern N. Amer. . . . . punctata (Banks), p. 29.
Apex of tenth tergum long, spatulate from above, acute in lateral view (Fig. 45). Great Lakes region, N. Amer. . . . . uvalo (Ross), p. 30.

15. Mesal ridge of coxopodite forming a setose knob (Fig. 48C); phallic parameres present (Fig. 48D). 17
Mesal ridge of coxopodite low, not knob-like (Fig. 46C); phallic parameres absent (Fig. 46D). 16

16. Apex of tenth tergite pointed in dorsal view, truncate in lateral view; ventral lobe of coxopodite 1/2 as long as base of coxopodite is wide (Resh, 1974, figs. 1-3). Illinois, N. Amer.. . . . . spongillovorax (Resh), p. 30.
Apex of tenth tergite rounded in dorsal view (Fig. 46B) and in lateral view (Fig. 46A); ventral lobe of coxopodite 1/4 as long as base of coxopodite is wide. Eastern N. Amer. . . . . maculata (Banks), p. 30.

17. Phallic parameres long, curved dorsad; ventral lobe of coxopodite long (Fig. 47). Western Palearctic Region . . . . . senilis (Burmeister), p. 30.
Phallic parameres reduced; ventral lobe of coxopodite not evident (Fig. 48). Eastern N. Amer.. . . cancellata (Betten), p. 30.

18. Tenth tergum sharply pointed in lateral view; mesal ridge of coxopodite with a bare, saber-like projection (Fig. 49). Ohio, N. Amer. . . . . erulla (Ross), p. 31.

Tenth tergum without narrow, acute subapico-ventral beak (Figs. 50A, 52A); mesal ridge of coxopodite either not projecting, or not bare or saber-like (Fig. 53C) 19

19. Extra lateral lobes of tenth tergum broadened apically; apex of tenth tergum hatchet-shaped (Fig. 50A). Wyoming, N. Amer. . . . . copha (Ross), p. 31.

Extra lateral lobes of tenth tergum absent or acute (Fig. 53A); apex of tenth tergum not so broadened. 20

20. Lateral lobes of tenth tergum with long, stout setae (Figs. 54A, 56A). .23

Lateral lobes of tenth tergum bare (Fig. 52A) 21

21. Extra lateral lobes of tenth tergum long, nearly straight; phallic parameres enlarged and bent apically (Fig. 51). Europe . . . . . ramburi Morse, n. sp., p. 31.

Extra lateral lobes of tenth tergum absent, shorter, or markedly upturned (Fig. 53A); phallic parameres not clavate (Fig. 52D). . .22

22. Tenth tergum with apico-dorsal sensilla and without long extra lateral processes; mesal ridge of coxopodite not projecting (Fig. 52). Palearctic Region and northwestern N. Amer. . . . . nigronervosa (Retzius), p. 32.

Tenth tergum bare apico-dorsally and with a pair of long, upturned, acute extra lateral processes; mesal ridge of coxopodite saw-like (Fig. 53). Northeastern N. Amer.. . . . . erratica (Milne), p. 32.

23. Lateral lobes of tenth tergum strongly separated from mesal portion; phallic parameres long and slender (Fig. 54). Northeastern N. Amer. . . . . albosticta (Hagen), p. 32.

Lateral lobes of tenth tergum situated tightly against main portion (Fig. 57A); phallic parameres short and broad (Fig. 57D) .24

24. Tenth tergum high, arching, broad in lateral view (Fig. 55A). Northeastern N. Amer. . . . . mentiea (Walker), p. 33.

Tenth tergum long, below level of superior appendages (Fig. 56A) . . .25

25. Pair of dorsal projections of tenth tergum triangular, directed anteriorly or dorsad; phallic parameres broad, downcurved (Fig. 56). Central and southeastern N. Amer. . . . . slossonae (Banks), p. 33.

Pair of dorsal projections longer, directed posteriorly; phallic parameres more slender, upturned apically (Fig. 57). Central and southeastern N. Amer.. . . . ophioderus (Ross), p. 33.

Key to Species of Ceraclea (Athripsodina)* (Males Only)

1. Ventral apex of phallobase cleft (Fig. 84E). 2

Ventral apex of phallobase entire with a long sclerite fused to the apical lip and ordinarily resting partly inside lower apical portion (Fig. 71D). North central N. Amer.. . . . . arielles (Denning), p. 38.

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*Species not keyed include major (Fig. 104), Kwangsi, China; mitis (Fig. 105), Japan; norfolki, Spain; and signaticornis (Fig. 106), Kuangtung, China.

2. Superior appendages long and slender, 5-6 times as long as wide, and separated basally (Figs. 63A, 63B) . . . . . Spinosa Group, 3
Superior appendages no more than 3 times as long as wide (Fig. 100B) and closer together or fused basally. 5
3. Bases of coxopodites not especially long anteriorly; fused harpago with single acute apical projection (Fig. 63). L. Tanganyika, Afr.. . . . . microbatia (Marlier), p. 35.
Bases of coxopodites elongate anteriorly (Fig. 64A); fused harpago with rounded dorsal process and dark mesal point (Fig. 64C) 4
4. Mesal projection of tenth tergum only 1/2 as long as superior appendages or tenth tergal processes (Fig. 64). Zaire, Afr.. . . . . batia (Mosely), p. 36.
Mesal projection of tenth tergum about as long as superior appendages or tenth tergal processes (Fig. 65). Zaire, Afr.. . . . . spinosa (Navás), p. 36.
5. Phalicata present, distinct; phallic parameres each with subapical annulation (Fig. 68D). . . . . Tarsipunctata Group, 6
Phalicata inconspicuous; phallic parameres, if present, deeply withdrawn into phallobase and not easily extruded, without subapical annulations (Fig. 72D) 10
6. Baso-ventral margin of coxopodite rounded without distinct process (Fig. 66). Minnesota, N. Amer. . . . brevis (Etnier), p. 37.
Baso-ventral process of coxopodite long, acute (Fig. 69A). 7
7. Lateral tenth tergal processes long, curved, each with obliquely truncate apex; phallobase with pair of rounded lateral projections above wide oblique groove (Fig. 67). North central and northeastern N. Amer. . . . . alagma (Ross), p. 37.
Lateral tenth tergal processes acute apically (Fig. 69A); phallobase without projections above oblique groove (Fig. 68D) . . 8
8. Phallic parameres upturned apically; periphallic processes rounded, 1/3 as long as phallobase (Fig. 69D) 9
Phallic parameres gradually downcurved; periphallic processes hardly evident in lateral view (Fig. 68D). Northern and eastern N. Amer. . . . . tarsipunctata (Vorhies), p. 37.
9. Lateral tenth tergal processes short and strongly curved upward and laterally; main portion of tenth tergite clavate with subapical dorsal margin concave in lateral view (Fig. 69). Central N. Amer. . . . . nepha (Ross), p. 37.
Lateral tenth tergal processes long, extending to apical enlargement of main piece; main portion of tenth tergite nearly straight dorsally (Fig. 70). Southeastern N. Amer. . . . . protonepha Morse and Ross, n. sp., p. 37.
10. Phallic paramere spines apparently absent (Fig. 91D). Ceylon . . . . . isurumuniya (Schmid), p. 44.
At least one retracted phallic paramere spine present (Fig. 84D). . . . 11
11. Three paramere spines apparently present; lateral lobes of tenth tergum as long as main portion of tergum and distinct nearly to the base (Fig. 107). Burma. . ungulifera (Kimmins), p. 48.
Only one or two paramere spines present (Figs. 95D, 97D); lateral lobes of tenth tergum not as long or as completely separated (Fig. 88A) 12

12. One retracted paramere spine present or two spines present but one small, 1/4 as large as the other spine or smaller (Figs. 80D, 81D, 84D, 97D) 33
    Two retracted paramere spines present and of approximately the same size, sometimes with one aligned before the other (Figs. 74D, 78D, 88D, 90D, 100D) 13
13. Semimembranous subapico-dorsal lobe of coxopodite present; harpago present (Figs. 72A, 78C) 15
    Semimembranous subapico-dorsal lobe of coxopodite very reduced, positioned inconspicuously on mesal surface of coxopodite; harpago absent (Figs. 99A, 99C). 14
14. Functional clasper very long, curved and acute (Fig. 98). Rewa, India . . . . . martynovi (Forsslund), p. 46.
    Functional clasper short with rounded subapico-ventral projection and apical crown of seta-bearing teeth (Fig. 99). Pusa, India . . . . . marginata (Banks), p. 46.
15. Ventral lobe of coxopodite as large as, or larger than, main body of coxopodite and with large or stout apical spine or spines (Figs. 88A, 88C). 25
    Ventral lobe of coxopodite either absent or much smaller and without apical spines (Figs. 75A, 72A, 108A) 16
16. Ventral lobe of coxopodite absent (Fig. 100). Southeastern China . . . . . dingwuschanella (Ulmer), p. 46.
    Ventral lobe of coxopodite present though often short (Figs. 78A, 108A). 17
17. Ventral lobe of coxopodite very slender and acute (Fig. 108). Amur region, Siberia . . . . . variabilis (Martynov), p. 48.
    Ventral lobe of coxopodite thicker, rounded or truncate apically (Figs. 75A, 75C, 78A, 78C) 18
18. Left paramere spine retracted far anterior of right spine and ventral margin of phallobase with semicircular excision in lateral view (Fig. 78D); ventral lobe of coxopodite very short (Fig. 78A); tenth tergum with pair of high sensilla-bearing ridges apically (Fig. 78A) . . . . . Diluta Group, 24
    Left paramere spine retracted to about same depth as right spine and phallobase not so excised (Fig. 72D); ventral lobe of coxopodite longer, often truncate apically (Fig. 77A); tenth tergum without apical ridges (Fig. 72A). . . . . Dissimilis Group, 19
19. Tenth tergum with slender lateral processes; ventral lobe of coxopodite short, rounded apically (Fig. 72). North central N. Amer. . . . . wetzeli (Ross), p. 39.
    Tenth tergum without lateral processes; ventral lobe of coxopodite long, truncate apically (Fig. 74A) 20
20. Ventral lobe of coxopodite straight from near its origin to before its apex; harpago as long as semimembranous subapico-dorsal lobe of coxopodite (Fig. 73). Japan . . . . . miyakonis (Tsuda), p. 39.
    Ventral lobe of coxopodite gradually curved; harpago smaller (Fig. 77A) 21
21. Tenth tergum with ventral margin slightly concave just before apex, tergum not strongly upturned (Fig. 74A). Pyrenees,

Europe . . . . . sobradieli (Navás), p. 39.
Tenth tergum rounded ventrally, strongly upturned (Fig. 75A) 22
22. Ventral lobe of coxopodite far from mesal ventro-basal margin, the lobes of the two inferior appendages widely separated in caudal view (Fig. 75C). Europe . . . dissimilis (Stephens), p. 39.
Ventral lobes of coxopodites nearly touching posteriorly (Figs. 76C, 77C) 23
23. Superior appendages broad and rounded apically in dorsal view; ventral lobe of coxopodite downcurved apically (Fig. 76). Szechwan, China . . . . . indistincta (Forsslund), p. 39.
Superior appendages narrow apically in dorsal view; ventral lobe of coxopodite upturned apically (Fig. 77). Amur region, Siberia. . . . . lobulata (Martynov), p. 40.
24. Light colored species; forewing of male 8.5-10.0 mm. long; mesal ridge of coxopodite strongly projecting (Fig. 78C). North central and eastern N. Amer. . . . . diluta (Hagen), p. 40.
Dark species; forewing of male 12-13 mm. long; mesal ridge of coxopodite short, rounded (Fig. 79C). Northern Europe . . . . . perplexa (MacLachlan), p. 40.
25. Ventral lobe of coxopodite with apical spines small (Figs. 88C, 89C) . . 26
Ventral lobe of coxopodite with apical spine or spines at least 1/3 as long as lobe (Figs. 90C, 93A) 27
26. Phallus large, the anterior half about twice as large as posterior half (Fig. 88D). Central Europe . . . riparia (Albarda), p. 43.
Phallus small, the anterior half about as large as posterior half (Fig. 89D). Foochow, China. . . . . yangi (Mosely), p. 43.
27. Lateral processes of tenth tergum each with very large subapical spine (Fig. 90B). Borneo . . . . modesta (Banks), p. 44.
Lateral processes of tenth tergum absent or with small apical setae (Fig. 92B) 28
28. Ventral lobe of coxopodite with two large spines, one apical and the other subapical (Fig. 93A) 29
Ventral lobe of coxopodite with a single large apical spine (Fig. 95A) 30
29. Ventral lobe of coxopodite as long and broad as main body of inferior appendage; mesal ridge of coxopodite without rounded projection on caudal surface (Fig. 92). Szechwan, China . . . . . forcipata (Forsslund), p. 44.
Ventral lobe of coxopodite smaller than rest of inferior appendage; mesal ridge of coxopodite with rounded setose projection on caudal surface (Fig. 93). Central and eastern N. Amer. . . . . flava (Banks), p. 44.
30. Ventral lobe of coxopodite broad, its apical spine as long as the lobe and strongly downcurved (Fig. 94). Japan. . . . . kamonis (Tsuda), p. 45.
Ventral lobe of coxopodite slender, its apical spine no more than 1/2 as long as the lobe (Fig. 95A) 31
31. Superior appendages divergent; tenth tergum truncate from above, acute from the side (Figs. 95A, 95B). 32
Superior appendages with apices narrower and closer together; tenth tergum rounded apically (Figs. 96A, 96B). Kiangsu, China . . . . . nankingensis (Hwang), p. 45.

32. Tenth tergum narrow in lateral view, its greatest width about 1/3 its length; ventral lobe of coxopodite angled posteriorly in ventral view and not curved mesad; harpago short and thick (Resh, 1974, figs. 8 and 11, not 9 and 10 as in caption). Kentucky and Virginia, N. Amer. . . . . neffi (Resh), p. 45.
Tenth tergum broader, its greatest width about 1/2 its length (Fig. 95A); ventral lobe of coxopodite curved mesad (Ross, 1944, fig. 774C); harpago longer and thinner (Fig. 95). Central and eastern N. Amer. . . . . .ancylus (Vorhies), p. 45.
33. Harpago and semimembranous subapico-dorsal lobe of coxopodite present, though often small (Figs. 80A, 84C) 34
Harpago and semimembranous lobe absent, with the huge ventral lobe serving as the functional clasper having an apical crown of seta-bearing teeth (Fig. 97C). Foochow, China . . . . . .fooensis (Mosely), p. 46.
34. Ninth sternum with a pair of long, slender processes (Fig. 102E) . . .35
Ninth sternum without long processes 36
35. Lateral processes of tenth tergum broad apically, more or less parallel to tergum (Fig. 101). Amur region, Siberia. . . . . .ensifera (Martynov), p. 47.
Lateral processes of tenth tergum slender apically and curved mesad over tergum (Fig. 102B). Chekiang, China . . . . . kashingensis (Tsuda), p. 47.
36. Lateral lobes of tenth tergum broad; ventral lobe of coxopodite absent (Fig. 103). Southeastern China . . . kolthoffi (Ulmer), p. 47.
Lateral lobes of tenth tergum absent or slender (Figs. 81A, 80A); ventral lobe of coxopodite at least as large as in Fig. 84A. . . . . Annulicornis Group, 37
37. Harpago large, nearly as long as semimembranous subapico-dorsal lobe of coxopodite (Figs. 80A, 81A) 38
Harpago much smaller (Fig. 83A). 40
38. Tenth tergum with slender lateral processes; ventral lobe of coxopodite long, dark apically, but without differentiated distal projection (Fig. 80A). Central Europe . aurea (Pictet), p. 41.
Tenth tergum without lateral processes (Fig. 81A); ventral lobe of coxopodite short with outcurved apical spine or process (Figs. 81A, 81C, 82A, 82F) 39
39. Superior appendages extending well beyond apex of ninth tergum; apical process of ventral lobe of coxopodite semimembranous and strongly outcurved (Fig. 81). Amur region, Siberia . . . . . sibirica (Ulmer), p. 41.
Superior appendages very short, hardly extending past apex of ninth tergum; apical process of ventral lobe of coxopodite well sclerotized and nearly straight (Fig. 82). Korea . . . . . .hastata (Botosaneanu), p. 41.
40. Proximal end of phallobase only slightly larger than distal end; phallobase strongly arched in middle; ventral lobe of coxopodite slender and only 2/3 as long as main body of inferior appendage (Fig. 83). Holarctic Region . . . excisa (Morton), p. 42.
Proximal end of phallobase greatly enlarged (Fig. 85D); phallobase not so strongly arched (Fig. 84D) or ventral lobe of coxopodite at least as long as main part of inferior appendage

(Figs. 85A, 86A) 41
41. Ventral lobe of coxopodite short, 1/3 as long as main body of inferior appendage; phallic guide not especially broad (Fig. 84). Holarctic Region. . . . . annulicornis (Stephens), p. 42.
Ventral lobe of coxopodite at least as long as main body of inferior appendage; phallic guide broad (Fig. 85C) 42
42. Ventral lobe of coxopodite slender most of its length and rounded apically (Fig. 85A). Northeastern N. Amer. . ruthae (Flint), p. 42.
Ventral lobe of coxopodite broad basally, tapering to very acute apex (Fig. 86C, 87A) 43
43. Tenth tergum sharply upturned in the middle; ninth tergum acute apically (Fig. 86). Mongolia. . . . . bicalcarata (Schmid), p. 42.
Tenth tergum gently curved and extended posteriorly; ninth tergum truncate apically (Fig. 87). Korea . . . . . shuotsuensis (Tsuda), p. 43.

Synopsis of Ceraclea, Its Subgenera, Species Groups, and Species

Complete bibliographies, including synonyms, of each species described before 1961 can be found in Fischer's monumental Trichopterorum Catalogus, vols. VI and VII (1965, 1966, covering literature through 1950) and XIV (1972, covering literature from 1951 through 1960). No attempt will be made here to complete these bibliographies to the present. However, all species described since 1960, as well as new synonyms and significant redescriptions, are included. Synonyms listed by Fischer are not repeated here unless a new opinion has been reported.

Each species listed below, except the type species and two new species, is to be regarded as a new combination.

The sex, repository city or private collection owner, and type locality of each type is indicated, respectively, following the original description citation of the different species.

Genus Ceraclea Stephens, 1829

Type species: Phryganea nervosa Fourcroy, 1785 (monobasic)
(a synonym of Ceraclea nigronervosa (Retzius), 1783)

Ceraclea Stephens, 1829: 28. Derivation or meaning unknown. Gender feminine according to usage by Stephens.

The history of the use of this generic name and the characters by which the larvae, pupae, and adults of Ceraclea and Athripsodes may be distinguished have been given by Morse and Wallace (1975). A couplet for separating adult males of the two genera is presented in the key to Ceraclea subgenera on page 17 above. Detailed descriptions of the different stages may be found in the section on morphology beginning on page 6 above.

Subgenus Ceraclea Stephens, 1829

This subgenus, composed of 30 species, is strictly Holarctic in distribution, with over 2/3 of its species confined to North America. One species is known from both North America and the Palearctic Region.

The species are generally larger and often darker than those in the subgenus Athripsodina. All of its known species except submacula have a separate, well-sclerotized phalicata. All except submacula and most of the Fulva Group species have a long ventral lobe of the phallobase. Only two paramere spines are present in all species except maculata, which has none. These spines are very reduced in submacula and cancellata. The semimembranous, subapico-dorsal lobe of the coxopodite is typically large and conspicuous. The extra lateral processes of the lateral tenth tergal lobes in the Nigronervosa Group arise on the surface of the lobes or tergite rather than on the lower edges or the basal angles of the tergite as is typical in the subgenus Athripsodina. The antennae of the larvae in this subgenus are usually shorter than in most Leptoceridae.

Fulva Group

The forewings of species in this group are various shades of brown, usually with a light patch at the arculus. All members have a short ventral apex of the phallobase except cama. All have characteristic lateral grooves on the phalicata where the parameres lie when the phalicata and parameres are retracted. The subapico-dorsal lobe of the coxopodite is bent caudad near its base. The harpago has a diagnostic subapical triangular projection. The tenth tergite is divided apically into a pair of large lateral lobes and a smaller median finger-like lobe which is itself divided in some specimens.

All the known larvae of species in this group feed on freshwater sponge, apparently as a necessary part of their life cycle (Resh, Morse, and Wallace, 1975). The lines demarking the parafrontal regions are obscure posteriorly and the antennae are only two times as long as broad. The case is made up almost entirely of salivary secretions (Lepneva, 1966).

Ceraclea (C.) cama (Flint)
(Fig. 33)

Athripsodes cama Flint, 1965: 174; male; Washington; Lake Waccamaw, North Carolina.

Distinguished from other species in the group by its long ventral apex of the phallobase, short parameres, short ventral lobe of coxopodite, relatively unconstricted apical tenth tergal lobes, and lack of a strong spine on mesal ridge of coxopodite. North Carolina, North America.

Ceraclea (C.) vertreesi (Denning)
(Fig. 34)

Athripsodes vertreesi Denning, 1966: 237; male; Denning collection, Moraga; Roseburg, Oregon.

Distinguished by very long ventral lobe of coxopodite and straight, thin apical 2/3 of each paramere, narrowed abruptly subapically. Oregon and British Columbia, North America.

Ceraclea (C.) biwaensis (Tsuda and Kuwayama)
(Fig. 35)

Leptocerus spinosus Tsuda, 1942b: 293; holotype not selected; presumably at Nara; syntypes from Keage, Kyoto, and Ôtsu, Shiga, Japan. Name preoccupied by Navás, 1930.

Leptocerus biwaensis Tsuda and Kuwayama, 1950: 420; first use of this name.

Leptocerus biwaensis Tsuda and Kuwayama, 1954: 12; cited as new name for L. spinosus.

No specimens examined in this study. Ventral lobe of coxopodite long with two strong apical setae. Superior appendages especially short. Japan.

Ceraclea (C.) resurgens (Walker)
(Figs. 36, 36')

Leptocerus resurgens Walker, 1852: 70; male; London; St. Martin's Falls, Albany River, Hudson's Bay.

Athripsodes resurgens (Walker); Ross, 1944: 230.

Varies considerably transcontinentally from that illustrated by Ross (1944) and Fig. 36' (eastern form) to that shown in Fig. 36 (western form), with all intergrades nearer the north central part of the continent. Ventral lobe of coxopodite shorter and with fewer spines, subapico-dorsal lobe shorter, and dorsal aspect of superior appendages broader and more truncate in western forms. Eastern forms with small central process of tenth tergite bifid. Northern transcontinental North America.

The species Leptocerus variegatus Hagen, 1861, is a synonym of resurgens as listed by Milne (1934). The lectotype of variegatus (Ross, 1938c) is without the spine on the mesal ridge of the coxopodite that was mentioned by Betten (1934).

Ceraclea (C.) alces (Ross)
(Fig. 37)

Athripsodes alces Ross, 1941: 95; male; Urbana; Chippewa River at Moose Lake, Hayward, Wisconsin.

Apico-lateral lobes of tenth tergite much longer than mesal process and broader than in related species. Ventral margin of tenth tergite concave in lateral view. Phallic parameres short, bent ventrad. Inferior appendages each with ventral lobe long and with strong apical setae. North central North America.

Ceraclea (C.) alboguttata (Hagen)
(Fig. 38)

Leptocerus alboguttatus Hagen, 1860: 70, new species with L. bimaculatus Stephens in synonymy; male; Cambridge; London.

Ventral lobe of coxopodite long as in vertreesi, biwaensis, resurgens, and alces and with two long, strong apical spines. Mesal ridge of coxopodite with short, stout spine and phallic parameres short and curved as in fulva and albimacula. Apico-mesal process of tenth tergite short, broad in lateral view. Europe.

Lectotype. Stephens (1836) apparently thought that he was redescribing Linnaeus' species bimaculata (see albimacula below) and not a new one. Thus, contrary to Kimmins' (1964) assessment in the text following his redescription of the Stephens specimens, Hagen did not propose a replacement name for bimaculatus Stephens but rather a new one for the misidentified species. Consequently it was not necessary for Kimmins to select a type for Hagen's species from Stephens' collection as he did. Additionally, a "type" specimen, apparently unknown to Kimmins, is in the Hagen collection in the Harvard Museum of Comparative Zoology in Cambridge, Massachusetts. Since there is no reason to suspect that Hagen ever saw Kimmins' lectotype and lectoallotype specimens and since a least one Hagen type of the species has been

preserved, Kimmins' type designations are invalid (Internatn. Code Zool. Nomencl., Art. 74a(i)). The single male specimen at Harvard, bearing labels, "M. alboguttatus (on white paper in Rambur's (?) handwriting); Hagen (printed); L. alboguttatus Hagen, L. annulatus ? Steph., *Walker. (Hagen's handwriting); Type, 10958," is here designated the LECTOTYPE of Leptocerus alboguttatus Hagen.

Ceraclea (C.) transversa (Hagen)
(Fig. 39)

Leptocerus transversus Hagen, 1861: 279; female; Cambridge; Washington, D. C.
Leptocerus angustus Banks, 1914: 263. NEW SYNONYM.
Athripsodes angustus (Banks); Ross, 1944: 231.

Mesal ridge of coxopodite with very long spine. Phallic parameres about 2/3 as long as phalicata. Central and eastern North America.

Lectotypes. The female lectotype of L. transversus Hagen (Ross, 1938c) is certainly the female of the species so well known to North American workers as Athripsodes angustus. The only paralectotype of L. transversus is a female of C. cancellata.

Two type specimens of L. angustus Banks are in the Harvard Museum of Comparative Zoology at Cambridge, Massachusetts. The male bearing labels, "Type; Go Home Bay Ont. Canada; Station I VIII; Walker Coll; Type 11570," is here designated the LECTOTYPE. The male PARALECTOTYPE is an example of Ceraclea (Athripsodina) alagma (Ross), 1938a.

Ceraclea (C.) latahensis (Smith)
(Fig. 40)

Athripsodes latahensis Smith, 1962; 295; male; San Francisco; Moscow, Latah County, Idaho.

Very similar to transversa but ventral lobe of coxopodite shorter and phallic parameres as long as, or longer than, phalicata. Central western North America.

Ceraclea (C.) fulva (Rambur)
(Fig. 41)

Mystacida fulva Rambur, 1842: 509; female; Brussels; Paris.
Leptocerus turanicus Martynov, 1928: 458. NEW SYNONYM.
Athripsodes fulvus (Rambur); Kimmins, 1964: 158.

Short stout spine evident on mesal ridge of coxopodite. Superior appendages very broad. Apico-mesal process of tenth tergite deeply bifid. Phallic parameres very short, downcurved. Western Palearctic Region.

Ceraclea (C.) albimacula (Rambur)
(Fig. 42)

Leptocerus bimaculatus Stephens (nec L.), 1836: 197, (misidentification, see alboguttata, p. 27).
Mystacida albimacula Rambur, 1842: 509, partim; male; Brussels; Paris.
Leptocerus albo-guttatus Hagen; MacLachlan, 1877: 300.
Leptocerus albimacula (Rambur); Ulmer, 1907b: 42, type discussion.
Leptocerus alboguttatus Hagen; Esben-Petersen, 1916: 126.
Leptocerus alboguttatus Hagen; Mosely, 1939a: 151.
Athripsodes alboguttatus (Hagen); Kimmins, 1964: 162, designation of lectotype.

Closely resembles fulva but superior appendages smaller, apico-lateral lobes of tenth tergite more clavate with mesal lobe not bifid, and phallic parameres not quite as short or downcurved. Europe.

Lectotype. Ulmer (1907b) found three specimens in the De Selys Longchamps collection (repository of the Rambur collection) at the Royal Institute of Natural Sciences in Brussels over the label "albimacula." He considered the third example (specimen "c") as Rambur's albimacula type. This specimen is here designated the LECTOTYPE of Mystacida albimacula Rambur, 1842. It now bears labels, "Mystacides albimacula; Ramb.; mystacides albimacula; Leptocerus bimaculatus St. McL.; M. albimacula R.; Collection Selys, Leptocerus albimacula Rb. Type, Revision Ulmer 1907, Leptocerus alboguttatus Hag.; Leptocerus alboguttatus Hg , + ; Type, Leptocerus albimacula Rb. (nec M. L.); Type." The other two specimens are ramburi (see below).

Submacula Group

The eyes of the males are huge and nearly contiguous dorsally. Those in the female are only slightly enlarged. The dorsal pair of facial warts has white setae. The forewings have scattered white scales over most of each wing, especially near the anastomosis, with one cluster before the stigma and another at the arculus. The forewings are dark brown otherwise. Only one species is known in the group.

Ceraclea (C.) submacula (Walker)
(Fig. 43)

Leptocerus submacula Walker, 1852: 70; male; London; St. Lawrence River.
Athripsodes submacula (Walker); Ross, 1944: 235.

Ninth abdominal segment with sternum narrow. Superior appendages small. Tenth tergite narrowed apically, acute in dorsal aspect. Subapicodorsal lobe of coxopodite dark, sclerotized. Harpago shaped like a battle axe. Phallus reduced, not at all like usual form in this subgenus. Phallobase long, curved, entire apically with a ventral subapical point. Phallic parameres very reduced. Definitive phalicata absent. Great Lakes region, North America.

Senilis Group

Wing coloration variable, from very dark (punctata) to very light (senilis) brown. Superior appendages broad basally. Tenth tergite without extra processes. Inferior appendage with short, rounded ventral lobe, except in cancellata. Ventral apex of phallobase longer than phalicata, dorsal apex divided into pair of long sclerotized plates.

Ceraclea (C.) punctata (Banks)
(Fig. 44)

Mystacides punctata Banks, 1894: 180; female; Cambridge; Douglas County, Kansas.
Athripsodes punctatus (Banks); Ross, 1944: 234.

White scales in a long, transverse triangle before the stigma, in a cluster at the arculus, and scattered over the distal 1/3 of the forewing. Lateral margins of tenth tergite broadly excised. Harpago large, gradually curved mesad. Central and northeastern North America.

Ceraclea (C.) uvalo (Ross)
(Fig. 45)

Athripsodes uvalo Ross, 1938b: 89; male; Urbana; Susquehanna River, Athens, Pennsylvania.

Very similar to punctata except tenth tergite longer and more broadly excavated, appearing very narrow apically in side view. Superior appendages more rounded ventrally, and harpago straighter basally. Central eastern North America.

Ceraclea (C.) maculata (Banks)
(Fig. 46)

Leptocerus maculatus Banks, 1899: 214; female; Cambridge; Washington, D.C.
Leptocerus inornatus Banks, 1914: 263; Flint, 1966: 383.
Athripsodes transversus (Hagen); Ross, 1944: 233.

White hairs interspersed with brown hairs on forewing to produce irrorate pattern. Pale region at arculus. Harpago slender, Phallic parameres absent. Central and eastern North America.

This common species has been known to North American workers as Athripsodes transversus for many years. However the female lectotype of transversus is actually a specimen of the species widely called A. angustus.

Ceraclea (C.) spongillovorax (Resh)

Athripsodes spongillovorax Resh, 1974: 267; male; Urbana; Apple River, Apple River Canyon, Jo Daviees County, Illinois.

Similar to maculata in many respects but differing in subtle details of male genitalia. Apex of tenth tergite pointed in dorsal view and truncate in lateral view, not rounded as in maculata. Ventral lobe of coxopodite long, 1/2 as long as coxopodite is wide. This lobe in maculata is only about 1/4 as long as coxopodite is wide. Illinois, North America.

Ceraclea (C.) senilis (Burmeister)
(Fig. 47)

Mystacides senilis Burmeister, 1839: 920; holotype not selected; presumably at Halle; syntypes from Berlin, Halle on the Saale, and Leipzig.
Athripsodes senilis (Burmeister); Kimmins, 1964: 160.

Forewings almost unicolorous light brown. Veins much less distinct in undenuded specimens than is the usual case in this subgenus. Tenth tergite with rounded ridge paralleling each ventro-lateral edge. Small setose knob on mesal surface of coxopodite. Harpago slender. Phallic parameres fused for about 1/2 their length. Larvae found in sponge (Nielsen, 1948; Lepneva, 1966; Resh, Morse, and Wallace, 1975). Western Palearctic Region.

Ceraclea (C.) cancellata (Betten)
(Fig. 48)

Leptocerus cancellatus Betten, 1934: 256; male; Albany; Saranac Inn, New York.
Athripsodes cancellatus (Betten); Ross, 1944: 233.
Athripsodes improcerus Edwards, 1956: 15. NEW SYNONYM.

Color pattern similar to that of maculata except light and dark areas usually a little larger. Mesal surface of coxopodite with setose knob. Ventral process of inferior appendage absent. Harpago slender. Phallic parameres short, but present. Central and eastern North America.

Nigronervosa Group

Generally large, dark species with wing veins particularly conspicuous (except mentiea, slossonae, and ophioderus). Species with white scales (erulla, erratica, and albosticta) have them scattered generally over the forewing except clusters at arculus and before stigma. Males of all members of this group have pair of large, lateral, sclerotized, ear-like lobes differentiated from main body of tenth tergite. In many species each of these lobes bears an additional process. Phallic parameres of all species except erulla have fine silky setae. Known females have mesal sclerite on ninth sternum between lateral plates.

Ceraclea (C.) erulla (Ross)
(Fig. 49)

Athripsodes erullus Ross, 1938b: 90; male; presumably at Columbus; Gibraltar Island, Put-in-Bay, Ohio.

White scales scattered over otherwise dark forewings. Center of face below antennae with tan setae, brown elsewhere on head. Tenth tergite with sharp apical points best seen in lateral view and with simple pair of ear-like lateral lobes. Mesal ridge of coxopodite produced apically in a long sharp process. Phallic parameres long, straight, acute. Ohio, North America.

Ceraclea (C.) copha (Ross)
(Fig. 50)

Athripsodes cophus Ross, 1938a: 156; male; Urbana; Green River north of Pinedale, Wyoming.

Forewings dark with brown setae, no white scales. Light tan setae on vertex and dorsal pair of facial warts, otherwise brown. Apex of tenth tergite hatchet-shaped in lateral view. Pair of extra lateral projections broad, especially distally. Harpago abruptly narrowed subapically. Wyoming, North America.

Ceraclea (C.) ramburi Morse, new species
(Fig. 51)

Mystacida albimacula "varieté" Rambur, 1842: 509; male; Brussels; Paris.
Leptocerus albimacula (Rambur); MacLachlan, 1877: 298; 1880: 63, (misidentification).
Leptocerus albimacula MacLachlan; Ulmer, 1907b: 42, type discussion.

Male. Length 12.0 mm. Center of face with white setae, sides with brown, vertex and notum with white and brown intermixed. Forewings with intermixed white and brown setae giving a hoary appearance except white at arculus. Superior appendages short. Tenth tergite long with a pair of straight, acute lateral processes nearly as long as main tergite. Ventral lobe of coxopodite broad, tapering to a small point. Harpago large and as long as the semimembranous subapico-dorsal lobe of the coxopodite. Phalicata with pair of lateral grooves. Phallic parameres capitate, each with apex bent and bearing several silky setae. Female unknown.

Holotype. Rambur's description of his albimacula "varieté" agrees with two specimens over the label "albimacula" in the Brussels collection which Ulmer (1907b, specimens "a" and "b") thought to have been the specimens subsequently identified by MacLachlan (1877, 1880) as Leptocerus albimacula (Rambur). Both specimens are in the De Selys Longchamps collection at the

Royal Institute of Natural Sciences in Brussels. Since, according to the above lectotype designation of albimacula and MacLachlan's misidentification, this species is without a name, it is here named Ceraclea (C.) ramburi Morse, new species. The holotype (Ulmer's specimen "a") now bears labels, "Mystacides albimacula; Hagen; 333; Collection Selys Type, Leptocerus albimacula M. L., Revision Ulmer 1907, Leptocerus albimacula M. L.; Leptocerus albimacula McL., nec Rbr., +; Type, Leptocerus albimacula M. L., (nec Rb.); Type."

Two paratypes include Ulmer's specimen "b" with labels, "M. albimacula, * Type Hagen or R.; +Leptocerus albimacula McL. ?, nec Rbr. !; Collection Selys, Leptocerus albimacula M. L., Revision Ulmer 1907, Leptocerus albimacula M. L. ?" and a specimen in the Harvard Museum of Comparative Zoology in Cambridge with labels, "mai; mystacides albimacula; Hagen; Type 10939."

Ceraclea (C.) nigronervosa (Retzius)
(Fig. 52)

Phryganea nigronervosa Retzius, 1783: 56; type sex unknown; presumably at Stockholm; Sweden (?).

Athripsodes nigronervosus (Retzius); Kimmins, 1964: 156.

Black species. Forewing membranes grey, venation fuscous, very conspicuous, without scales. Male head setae all brown. Center of face of females white to light tan, otherwise light brown. Tenth tergite short, the lateral ear-like lobes well-defined. Some specimens with vestigial triangular projection on lobes or body of tergite. Inferior appendage with broad, rounded ventral lobe. Phallic parameres short, with silky setae clustered around moderately well-differentiated apical spine. Larvae found in sponge (Nielsen, 1948; Resh, Morse, and Wallace, 1975). Transcontinental Palearctic Region and northwestern North America.

Ceraclea (C.) erratica (Milne)
(Fig. 53)

Athripsodes erraticus Milne, 1936: 58; male; Urbana; Chelsea, Quebec.

Athripsodes erraticus Milne; Ross, 1944: 235.

Dark, nearly black species. Forewings dark brown with veins conspicuous and with scattered white scales. Head setae of males and females mostly light brown to white in front, brown on vertex. Tenth tergite short, upturned, without sensilla; lateral ear-like lobes well-defined; extra lateral processes upturned, acute, nearly as long as tergite. Coxopodite with broadly rounded ventral lobe and saw-like mesal ridge with short stout setae. Harpago tiny. Phallic parameres fused a short distance basally and with silky setae clustered around large, stout apical spine. Great Lakes region, North America.

Many paratypes of this species are misidentified specimens of albosticta and other close relatives.

Ceraclea (C.) albosticta (Hagen)
(Fig. 54)

Leptocerus albostictus Hagen, 1861: 276; female; Cambridge; Winthem, North America.

Athripsodes saccus Ross, 1938b: 89. NEW SYNONYM.

Nearly black species. Forewings dark with scattered white scales. Head with many light brown and white setae. Tenth tergite very short, hardly

longer than short, broad superior appendages, and with strongly defined lateral lobes slightly longer, bearing stout setae. Mesal ridge of coxopodite large with a row of stout setae. Phallic parameres very long, slender. Great Lakes region, North America.

Ceraclea (C.) mentiea (Walker)
(Fig. 55)

Leptocerus mentieus Walker, 1852: 71; male; London; St. Martin's Falls, Albany River, Hudson's Bay.
Athripsodes mentieus (Walker); Ross, 1944, 232.

Brown, lighter than preceding species of the group. Forewings brown with light maculations at arculus and before the stigma. Superior appendages small. Tenth tergite short, tall, hood-shaped. Apical sensilla very short with two or three near base long. Ear-like lateral lobes not strongly defined, with long stout setae. Subanal plate long, projecting beneath the apex of tenth tergite. Mesal ridge of coxopodite broad with row of stout setae. Phallic parameres short, broad basally, tapering to acute point. North central and northeastern North America.

All subsequent workers through 1934 considered the species name a misspelling of the Latin masculine substantive "mentiens" (meaning "fallacy" or "sophism") intended for use in apposition. After 1934, the original spelling was readopted. Since there is no "clear evidence of an inadvertent error. . . in the original publication" (Intern. Code Zool. Nomencl., Art. 32a(ii)), I am following the opinion of more recent authors in considering the word a first declension Latin adjective.

Ceraclea (C.) slossonae (Banks)
(Fig. 56)

Athripsodes slossonae Banks, 1938: 77; male; Cambridge; Belleair, Florida.
Athripsodes daggyi Denning, 1948c: 254; Flint, 1966: 382.

Color similar to mentiea. Tenth tergite very long with sensilla arranged as in mentiea. Vestigial extra lateral processes of tenth tergum short, triangular, directed anteriorly or dorsally. Ear-like lateral lobes moderately conspicuous with stout setae. Subanal plate long. Mesal ridge of coxopodite small with scattered setae. Phallobase ventral projection spoon-shaped. Parameres each thick, narrowed apically or sometimes a short distance subapically to acute downcurved terminus. Central and southeastern North America.

Ceraclea (C.) ophioderus (Ross)
(Fig. 57)

Athripsodes ophioderus Ross, 1938a: 157; male; Urbana; Elizabethtown, Illinois.

Color similar to mentiea. Genitalia similar to slossonae (Flint, 1966). However, tenth tergite not so long and more rounded apically. Vestigial extra lateral processes of tenth tergum longer, strongly bent posteriorly. Apex of ninth tergite projects more posteriorly. Mesal ridge of coxopodite broad with setae in a row along dorsal edge. Ventral projection of phallobase spatulate, more nearly flat in lateral view. Parameres more slender, at least 3 times as long as broad, and upturned apically. Central and southeastern North America.

Unplaced Species of Ceraclea (Ceraclea)

The following comments are based wholly on published descriptions or on the examination of indeterminable female types.

Ceraclea (C.) distinguenda (Martynov)
(Fig. 58)

Leptocerus distinguendus Martynov, 1936: 251; male; presumably at Calcutta; Harra, Rewa State.

This species is probably a member of the Fulva Group as is indicated by the caudal bend at the base of the semimembranous subapico-dorsal lobe of the coxopodite, a feature peculiar to species of that group. If this is so, this species can be separated from other members of the group by the longer, bifid mesal projection of the tenth tergite which extends beyond its lateral apical lobes. Rewa, India.

Ceraclea (C.) floridana (Banks)

Leptocerus floridanus Banks, 1903: 242; female; Cambridge; Biscayne Bay, Florida.

The abdomen of the female type is missing. The left wings are mounted dry on a separate slide. White and brown setae occur on the forewings in small patches giving a salt and pepper appearance unlike any species now known from the southeastern United States. Florida, North America.

Ceraclea (C.) nygmatica (Navás)

Leptocerus nygmaticus Navás, 1917a: 8; female, Navás Collection, Zaragosa; Caesarea, Cappadocia.

Female holotype specimen much rubbed, but coloration is light, similar to senilis. However, the lateral grooves above the ninth sternum each have a more acute mesal extension, the distal flaps ("gonapophyses" of authors) are longer, and the bursal sclerite is longer than in senilis. The specimen probably is of a species closely related to senilis whose male is yet unknown. Eastern Turkey.

Ceraclea (C.) superba (Tsuda)
(Fig. 59)

Leptocerus superbus Tsuda, 1942b: 292; holotype not selected; presumably at Nara; syntypes from Keage and Kitaôji-bashi, Kamogawa, Kyoto, Japan.

No mention or illustration of the tenth tergite is given in the original description. The species is placed here in the subgenus Ceraclea because the large semimembranous subapico-dorsal lobe of the coxopodite and its large mesal ridge with short stout setae are shaped similar to these features in the Nigronervosa Group. Japan.

Subgenus Pseudoleptocerus Ulmer, 1907a

Type species: Leptocerus squamosus Ulmer, 1905 (monobasic)
(Figs. 60, 61, 62)

Species of this subgenus may be distinguished from others in Ceraclea by the long ventral margin of the phallobase and by the separate, sclerotized triangular region of the ninth sternum, sometimes highly modified.

The subgenus contains 11 species, all of which are known only from

Africa. Mosely (1933) reviewed the genus Pseudoleptocerus at a point in time when only 4 species were known. Kimmins (1956) reassessed its taxonomic limits and excluded minor on the basis of wing venation characteristics, giving the species the replacement name minimus because of the homonomy occasioned by inclusion of the species in his genus Athripsodes. This species and pulchra are included here in Pseudoleptocerus due to the above mentioned taxonomically and phylogenetically significant character states. The other species making up the subgenus are listed in the section on material studied on page 4.

The larva of Ceraclea (Pseudoleptocerus) schoutedeni (Navás) has been described by Marlier (1956) and Corbet (1958) and its case by Marlier (1954). Besides character states seen in other larvae of the genus Ceraclea, the head is especially large relative to the size of the body, and the parafrontal regions are absent.

Subgenus Athripsodina Kimmins, 1963
Type species: Leptocerus marginatus Banks, 1911
(original designation)

At least 48 species are included in this subgenus, all of which occur either in the Nearctic, the Palearctic, the Ethiopian or the Oriental Region. Two species have Holarctic distributions.

The species of Athripsodina are generally smaller than those in the subgenus Ceraclea and lighter colored than those in Pseudoleptocerus and Ceraclea subgenera. Males of Athripsodina have the ventral apex of the phallobase cleft (except arielles). The tenth tergite of many species has a pair of rod-like lateral processes which arise on the ventro-lateral edges of the tergite, unlike somewhat similar processes of the Ceraclea (C.) Nigronervosa Group. These processes are especially long in the Spinosa and Tarsipunctata Groups in which species they are separate from the main tergite nearly to the base. The processes have been lost independently at least 7 times (the Diluta Group, the sibirica-hastata line, the Arielles Group, dingwuschanella, variabilis, and within the Dissimilis and Marginata Groups). Generally the semimembranous subapico-dorsal lobe of the coxopodite and the harpago are smaller than in the subgenus Ceraclea. The phalicata is never a strongly defined tubular structure as is usual in the rest of the genus.

Spinosa Group

This group contains the only known African species of the subgenus. The superior appendages are peculiar for the genus in being very long and slender. The tenth tergite is without sensilla and is acute apically. The lateral processes of the tergite are as long as, or longer than, the mesal main portion. The fused bases of the inferior appendages are unusually long in batia and spinosa, with the basal plate fused to the anteriorly extended ventral portion of the phallic shield. The harpago is fused with the coxopodite and is apically bifid in batia and spinosa. The phalicata is very reduced in microbatia and inconspicuous or fused to the inner surface of the apical lobes of the phallobase in batia and spinosa. The periphallic processes and phallic parameres are absent. The pupa and case of microbatia have been described by Marlier (1956).

Ceraclea (Athripsodina) microbatia (Marlier)
(Fig. 63)

Leptocerus microbatia Marlier, 1956: 349; male; Tervuren; Uvira, Tanganika.

A tiny (forewing length 6.4 mm.), very pale species. Lateral processes of tenth tergite 1 1/2 times as long as mesal main portion. Fused region of bases of coxopodites and ventral lip of phallic shield not projecting anteriorly as far as in batia and spinosa. Harpago fused to coxopodite and tapering to acute apex. Phalicata poorly sclerotized and inconspicuous. Phallobase with a pair of rounded, longitudinal, dorso-lateral ridges especially pronounced apically. Uvira, Lake Tanganyika, Africa.

Ceraclea (Athripsodina) batia (Mosely)
(Fig. 64)

Leptocerus batia Mosely, 1939b: 6; male; Tervuren; Kiou, Kibati, Congo.
Leptocerus fuscus Jacquemart, 1961: 66. NEW SYNONYM.

Larger than preceding (forewing length 10.5-11.0 mm.), beige with an oblique gold stripe near base of forewing and with alternating light and dark regions along the apical fringe. Main body of tenth tergum 1/2 as long as lateral processes. Bases of coxopodites, together with phallic guides, as long as externally visible portion of inferior appendage in lateral view. Ventral portion of phallic shield projecting anteriorly 3/4 as long as phallobase. Pair of sclerotized lips just inside apical lobes of phallobase fused with phallobase lobes and with each other ventrally; possibly these are the vestigial phalicata. Zaire, Africa.

Ceraclea (Athripsodina) spinosa (Navás)
(Fig. 65)

Leptocerus spinosus Navás, 1930: 333; male; Tervuren; Albertville, Congo.
Leptocerus schoutedeni Mosely, 1939b: 14. NEW SYNONYM.
Leptocerus bispinosus Jacquemart, 1961: 66. NEW SYNONYM.

Smaller than preceding species (forewing length 8-9 mm.). Forewing chestnut color with lighter spot at apex. Mesal portion of tenth tergite abruptly narrowed just before middle, nearly as long as lateral processes, acute. Bases of coxopodites elongate anteriorly as in batia, but ventral portion of phallic shield not as long. A small triangular projection often present on caudal surface of coxopodite. Sclerotized lips inside apical lobes of phallobase larger, fused as in batia. Kalémié, Zaire, Africa.

The slender apical portion of the tenth tergite is broken away in the type of schoutedeni, giving the false impression of a distinct species.

Tarsipunctata Group

Similar in general appearance to members of the Ceraclea (C.) Fulva Group. The forewings various shades of brown with light brown hairs in small patches, especially at the arculus. Lateral processes of tenth tergite very long, upturned, and nearly or completely separate from the main body of the tergite. Coxopodites each with acute ventral lobe (except brevis), rounded setose mesal ridge, and harpago large. Both pairs of phallic parameres present, although dorsal pair usually reduced and easily confused with pair of reticulate semimembranous dorsal lobes of phalicata. Phalicata membranous dorsally, supporting endophallic membranes in manner of Mexican taco. Lateral parameres each with subapical annulation. Phallobase narrow near base with pair of deep, rounded, oblique grooves. Ninth sternum and phallic shield with sclerotized strips present, though not always articulating. Phallic

shield strips short, each with large, rounded, extrinsic posterior projection especially evident in nepha and related new species.

Ceraclea (Athripsodina) brevis (Etnier)
(Fig. 66)

Athripsodes brevis Etnier, 1968: 188; male; Urbana; Garrison Ranger Station, Crow Wing County, Minnesota.

Very similar to alagma except ventral lobe of coxopodite absent. Lateral processes of tenth tergum with obtuse, subapical angle. Apex of main body of tergum clavate in lateral view. Periphallic projections present, rounded. Pair of sclerotized longitudinal, rounded "wings" on either side of phallobase above oblique groove. Dorsal parameres fused in a partly sclerotized flap above phalicata. Minnesota, North America.

Semimembranous subapico-dorsal lobes of coxopodites not fully expanded in teneral holotype.

Ceraclea (Athripsodina) alagma (Ross)
(Fig. 67)

Athripsodes alagmus Ross, 1938a: 155; male; Urbana; Fox Lake, Illinois.

Very similar to brevis except ventral lobe of coxopodite normal for the group, acute. Periphallic projections hardly evident. North central and northeastern North America.

Ceraclea (Athripsodina) tarsipunctata (Vorhies)
(Fig. 68)

Leptocerus tarsi-punctatus Vorhies, 1909: 694; holotype not selected; syntype male at Cambridge; Wisconsin.

Athripsodes tarsi-punctatus (Vorhies); Ross, 1944: 229.

Main body of tenth tergite gradually tapered and downcurved in a rounded hood. Lateral processes not as curved as in brevis and alagma. Phallobase long, without lateral "wings." Lateral parameres very gradually downcurved. Dorsal parameres appearing as pair of weakly sclerotized paddles above phalicata. Northern and eastern North America.

Ceraclea (Athripsodina) nepha (Ross)
(Fig. 69)

Athripsodes nephus Ross, 1944: 230; male; Urbana; Des Plaines River, Rosecrans, Illinois.

Main portion of tenth tergite clavate apically in lateral view. Lateral processes 1/2 as long as main body, strongly curved dorsad. Periphallic projections long, digitate. Lateral parameres each upcurved beyond subapical annulation. Otherwise similar to tarsipunctata. Central North America.

The paratype collected with the holotype is a specimen of the following species.

Ceraclea (Athripsodina) protonepha Morse and Ross, new species
(Fig. 70)

Male. Length 9.0-10.0 mm. Head and thoracic sclerites and antennae medium reddish-brown. Legs and palps somewhat lighter. Tarsal segments darker apically. Wing membranes light brown. All specimens in alcohol so that wing setal coloration pattern indiscernible. General structure typical for genus.

Genitalia as in figure 70. Ninth tergum overhangs bases of superior appendages and tenth tergites. Superior appendages long, slender subapically. Mesal tenth tergite clavate in lateral view, with subapico-dorsal margin nearly straight. Lateral processes long, extending as nearly straight pieces to apical enlargement of mesal process. Inferior appendages and phallus similar to those of nepha.

Female. Length 9.0-10.0 mm. Indistinguishable from tarsipunctata and nepha.

Holotype. Male, Virginia, Norfolk Co., along north edge of Lake Drummond, Dismal Swamp, May 18, 1963, R. L. Hoffman. Deposited at I. N. H. S., Urbana, Illinois.

Paratypes. Florida: Okaloosa County, Blackwater River, 2.5 miles west of Holt, 24 April, 1970, W. L. and J. C. Peters, M. L. Pescador, J. Jones. Many males and females. Deposited in the Florida State Collection of Arthropods at Florida A. & M. University. Same but 8 May, 1970, 20 males. Deposited at U. S. N. M., Washington. Same except Peadton Bridge 4.5 miles northwest of Cannon Town, 25 April, 1970, 3 males. Deposited in the Fla. State Col. Arth. Georgia: Tift County, Little River at U.S. Rt. 82, 18 April, 1972 V. H. Resh and J. C. Morse, 98 males, many females. Deposited at U. S. N. M., Washington. Appling and Toombs County line, Altamaha River at U. S. Rt. 1, 8-10 April, 1974, Sherberger and Hager. Deposited at U. S. N. M., Washington.

This species is very similar to nepha except that the lateral processes of the tenth tergum are nearly straight and extend 3/4 the length of the mesal tergite. The mesal tergite is nearly straight along its subapico-dorsal margin in lateral view.

Arielles Group

Antennae brown, flagellum annulated with white at base of each proximal segment. Wings light brown with white mark at arculus. Only one species in the group is known.

Ceraclea (Athripsodina) arielles (Denning)
(Fig. 71)

Athripsodes arielles Denning, 1942: 48; male; St. Paul; Coon Creek, Anoka County, Minnesota.

Athripsodes pfadti Denning, 1948b: 17. NEW SYNONYM.

Superior appendages broad. Tenth tergite short, broad, upturned apically. Inferior appendages each with short ventro-basal lobe. Harpago disc-shaped apically. Phallobase forming large sleeve, not cleft apico-ventrally. Parameres lobes and spines partially retracted when at rest. Phalicata represented by a pair of semimembranous plates offset to the right. Ventral lip of phallobase protracted into a long, angled, sclerotized strip which rests below the parameres and phalicata when retracted; tilts apico-ventrally when phallic structures extruded, with the flat, anterior strip bending dorsad. North central North America.

Dissimilis Group

Head and thoracic sclerites reddish brown with predominately white setae. Forewings brown, darker apically, each with small white mark at arculus.

Superior appendages broad basally, fused for at least half their length. Tenth tergite short, without lateral processes (except wetzeli). Phallobase asymmetrical apically with left lobe narrower than right and curved ventrad. Dorsal sclerotized strip similar to that seen in arielles often evident. Paramere spines retracted to approximately the same depth within phallobase.

Ceraclea (Athripsodina) wetzeli (Ross)
(Fig. 72)

Athripsodes wetzeli Ross, 1941: 94; male; Urbana; Kettle Creek, Clinton County, Pennsylvania.

Superior appendages broad, slightly narrowed subapically, shorter than tenth tergite. Tenth tergite nearly truncate apically in lateral view, acute from above. Pair of lateral processes arise from sides of base of tergite rather than from lower edges as is usual in most of subgenus. Inferior appendage with short, rounded ventral lobe. Harpago small. Phallobase asymmetrical apically, but with left lobe not as narrow as in most species of Dissimilis Group. Northeastern North America.

Ceraclea (Athripsodina) miyakonis (Tsuda)
(Fig. 73)

Leptocerus miyakonis Tsuda, 1942b: 289; holotype not selected; presumably at Nara; syntypes from Keage, from Kamogawa, and from Arashiyama, Kyoto, also from Imazu, Shiga, Japan.

Superior appendages longer than tenth tergite. Tenth tergite upturned apically, without lateral processes. Ventral lobe of coxopodite very long. Japan.

Ceraclea (Athripsodina) sobradieli (Navás)
(Fig. 74)

Leptocerus sobradieli Navás, 1917b: 7; male; Navás collection, Zaragosa; Sobradiel, Zaragosa, Spain.

Superior appendages longer than tenth tergite. Tenth tergite broadly excavated laterally before apex; apex nearly straight in side view. Ventral lobe of coxopodite longer than in wetzeli. Left apical lobe of phallobase short, narrow, strongly hooked downward. Northern Spain and southern France.

Ceraclea (Athripsodina) dissimilis (Stephens)
(Fig. 75)

Leptocerus dissimilis Stephens, 1836: 190; male; London; Britain.
Athripsodes dissimilis (Stephens); Kimmins, 1964: 174.

Superior appendages longer than tenth tergite. Tenth tergite strongly upturned apically. Ventral lobe of coxopodite very long, truncate. Phallobase with left lobe not so strongly hooked as in sobradieli. Europe.

Ceraclea (Athripsodina) indistincta (Forsslund)
(Fig. 76)

Leptocerus indistinctus Forsslund, 1935: 8; male; Stockholm; I-chi-chang, Szechwan, China.

Similar to dissimilis except superior appendages rounded apically in dorsal view and ventral lobe of coxopodite smaller, slightly downcurved apically. Szechwan, China.

According to the curator, P. I. Persson, the type abdomen is probably lost.

Ceraclea (Athripsodina) lobulata (Martynov)
(Fig. 77)

Leptocerus lobulatus Martynov, 1935: 223; holotype not selected; type deposition unknown; syntypes from Amur, Zeja, and Bikin Rivers near Blagovestshensk, Siberia.

Superior appendages narrower apically than in indistincta in dorsal view. Ventral lobe of coxopodite small, upturned apically. Left lobe of phallobase acute, downcurved, but not strongly hooked as in sobradieli. Amur region, Siberia.

Diluta Group

Genitalia of two species composing this group very similar, but size and color differences quite marked. Superior appendages subtriangular. Tenth tergite without lateral processes, its apex with pair of high, sensilla-bearing ridges. Inferior appendages each with very short, rounded ventral lobe. Phallus short, with small, ventral, semicircular excision in lateral view. Left paramere spine about same size as right, but retracted much more deeply.

Ceraclea (Athripsodina) diluta (Hagen)
(Fig. 78)

Leptocerus dilutus Hagen, 1861: 277; male; Cambridge; Chicago, Illinois.
Leptocerus retactus Banks, 1914: 263. NEW SYNONYM.
Athripsodes dilutus (Hagen); Ross, 1944: 231.

Smaller than perplexa, forewing of male only 8.5-10.0 mm. long. Lighter, with head and thoracic sclerites light to reddish-brown with tan or white setae. Forewings medium brown with conspicuous light mark at arculus. Wing veins not especially conspicuous. Coxopodite with mesal ridge high, well-differentiated. North central and eastern North America.

Ceraclea (Athripsodina) perplexa (MacLachlan)
(Fig. 79)

Leptocerus perplexus MacLachlan, 1877: 302; holotype not selected; type deposition unknown; syntypes from St. Petersburg, Russia, and from East Bothnia and Kuusamo, Finland.

Male forewing 12-13 mm. long. Head and thoracic sclerites very dark reddish-brown or black. Forewings dark brown with very small light mark at arculus and veins quite conspicuous. Coxopodite with mesal ridge only slightly elevated, not protracted as in diluta. Paramere spines thinner and not as strongly sclerotized as in diluta. Northern Europe.

A note in the files of the British Museum (Natural History) in London indicates, "Type in Helsinki Mus. ?"

Annulicornis Group

Head and thoracic sclerites various shades of brown with light setae. In most species (except aurea, sibirica, and hastata), vertex and middle portion of mesonotum form dark mesal stripe with temporal regions and lateral portions of notum lighter. Proximal antennal segments annulated with white basally. Superior appendages generally short and tenth tergite long, upturned, and usually rounded apically. Inferior appendages either slender (most species) or broad basally (aurea, sibirica, and hastata), each with ventral lobe at

least as long as in annulicornis. Phallic guides of coxopodite usually broad and often rather long. Left paramere spine reduced in all species and seta-like in most species. Anterior end of phallobase greatly enlarged in annulicornis, ruthae, bicalcarata, and probably in shuotsuensis with large retracted left paramere lobe mostly filling it. Phalicata reduced to pair of semisclerotized plates offset to the right.

Ceraclea (Athripsodina) aurea (Pictet)
(Fig. 80)

Mystacide aurea Pictet, 1834: 164; male (?); type deposition unknown; Troinex, near Geneva.
Leptocerus aureus (Pictet); Martynov, 1924: 113.

Head and thorax fuscous with white and few golden brown setae. Forewings with rich golden-brown setae obscuring wing veins, with distal margin darker, and with slightly lighter spot at arculus. Superior appendages longer than in other Annulicornis Group species. Tenth tergite somewhat hatchet-shaped apically and with long lateral processes. Inferior appendages broad, each with long, curved ventral lobe dark apically. Harpago large, blunt. Phallic guides broad, short. Apico-lateral lobes of phallobase each with large, lateral triangular projection. Left paramere spine short, stout, deeply retracted. Europe.

A single male without abdomen is in the Natural History Museum in Geneva. The printed label is apparently a substitute for Pictet's and is not particularly helpful for recognizing his type. It is possible, however, that this is the single specimen which Pictet originally described (Zwick, 1971; Botosaneanu and Schmid, 1973).

Ceraclea (Athripsodina) sibirica (Ulmer)
(Fig. 81)

Leptocerus sibiricus Ulmer, 1906: 36; male; Leiden; Psiskia, Amur, Siberia.
Leptocerus sibiricus Ulmer; Martynov, 1935: 218.

Head and thorax uniformly dark reddish-brown, nearly black. Forewings with golden setae except brown setae in three patches: over stigma, in region of similar size beyond arculus, and in apical patch nearly as large as each of first two. Superior appendages short, fused basally. Tenth tergite without lateral processes. Coxopodites broad, each with moderately long ventral lobe terminated by short, semimembranous, outcurved process. Phallic guides very broad and long. Harpago larger than in aurea, much larger than in other species of group. Left paramere spine short, stout, beneath greatly enlarged right paramere spine. Phallobase short dorsally. Amur region, Siberia.

Lectotype. Two specimens (1 male, 1 female), are in the Albarda collection in the Netherlands National Museum of Natural History in Leiden. The male, bearing labels, "Amur, Psiskia; Leptocerus sp. descr. ♀; Coll. Albarda, aug. 1892; Leptocerus sibiricus Ulmer, 2 types!; Museum Leiden, Leptocerus sibiricus, Det. Ulmer; Cat. No. 1," is here designated the LECTOTYPE. The female PARALECTOTYPE bears labels, "Amur, Chabarofka; Leptocerus sp. descr. ♂; Coll. Albarda, aug. 1892; Museum Leiden, Leptocerus sibiricus, Det. Ulmer; Cat. No. 2."

Ceraclea (Athripsodina) hastata (Botosaneanu)
(Fig. 82)

Athripsodes hastatus Botosaneanu, 1970: 380; male; presumably at Warsaw;

Hjangam-ri, District Hjangsan-chon, Mts. Mjohjang-san, Korea.

Very similar to sibirica. Superior appendages much shorter. Apical process of each coxopodite lobe ("épine robuste") thinner and more strongly sclerotized. Korea.

Ceraclea (Athripsodina) excisa (Morton)
(Fig. 83)

Leptocerus excisus Morton, 1904: 67; holotype not selected; type deposition unknown; brook near Ekenäs, Finland.

Athripsodes perplexus nordus Milne, 1934: 15. NEW SYNONYM.

Athripsodes miscus Ross, 1941: 93. NEW SYNONYM.

Athripsodes scopulosus Leonard and Leonard, 1949: 6. NEW SYNONYM.

Head and thoracic sclerites dark fuscous. Forewings concolorous brown except small testaceous spot at arculus. Tenth tergite long, upturned and acute apically in lateral view. Lateral processes short. Inferior appendages thin, each with moderately long, slender ventral lobe rounded apically. Harpago tiny. Phallic guide variable. Phallus strongly curved ventrad. Left paramere spine seta-like. Northern Holarctic Region.

Ceraclea (Athripsodina) annulicornis (Stephens)
(Fig. 84)

Leptocerus annulicornis Stephens, 1836: 199; female; London; Britain.

Athripsodes annulicornis (Stephens); Ross, 1944: 232.

Dark mesal stripe of head and notum evident. Wings brown with light yellowish arculus mark more evident than in related species. Tenth tergite acute from above, and with short, finger-like lateral processes. Ventral lobe of each inferior appendage relatively short, rounded apically. Phallic guide not protracted. Phallobase very large and bulbous anteriorly. Seta-like left paramere spine often absent. Right paramere spine large with a sclerotized basal plate. Holarctic Region.

Ceraclea (Athripsodina) ruthae (Flint)
(Fig. 85)

Athripsodes ruthae Flint, 1965: 174; male; Washington; Fort River, East Amherst, Massachusetts.

Generally fuscous except pale at anal angle of forewing. Tenth tergite tapering and broadly rounded apically from above and with long slender lateral processes. Ventral process of coxopodite blunt apically, nearly as long as main body of inferior appendage. Mesal ridge of coxopodite produced into long, finger-like lobe. Phallic guides broad but not projecting. Phallobase bulbous anteriorly with retracted left spine seta-like. Ventral margin of phallobase with broad rounded excision in lateral view. Northeastern North America.

The apical processes of the pupa and the pupal case have been figured by Leonard and Leonard (1949, figs. 4, 9) from metamorphotypes misidentified as scopulosus.

Ceraclea (Athripsodina) bicalcarata (Schmid)
(Fig. 86)

Athripsodes bicalcaratus Schmid, 1970a: 121; male; presumably at Warsaw; River Delger Mörön, 8 km. north of Somon Burenchaan, Hövsgol Province, Mongolia.

Dorsal stripe reddish-brown, lateral areas fulvous. Forewings reddish-

brown, each with opaque testaceous stigma. Superior appendages short, fused most of their length. Tenth tergite upturned from the middle, acute from above, and with short, slender lateral processes. Ventral lobe of each coxopodite long, broad basally, acute apically; phallic guides broad, projecting; setose mesal ridge as long as broad. Phallus similar to that of ruthae, but with acute ventral angle about midway. Mongolia.

Ceraclea (Athripsodina) shuotsuensis (Tsuda)
(Fig. 87)

Leptocerus shuotsuensis Tsuda, 1942a: 233; male; presumably at Nara; Shuotsu, northern Korea.

Very similar to bicalcarata. Ninth tergite truncate rather than acute apically. Superior appendages nearly as long as tenth tergite. Tenth tergite not as strongly bent dorsad as in bicalcarata. Korea.

Riparia Group

Color pattern consistently light reddish-brown head and thorax and concolorous light brown forewings (except modesta and isurumuniya). Superior appendages relatively short and usually fused basally. Tenth tergite of various shapes and usually bearing pair of slender lateral processes. Inferior appendages each with very strong ventral lobe positioned at acute angle with respect to main body of coxopodite. This lobe with at least one and as many as three strong spines, two of which are apical with third subapical on ventral margin. Paramere spines (absent in isurumuniya) lined up in a peculiar fashion: left (anterior) spine with its apex usually inserted into eliptical opening at base of right (posterior) spine. All specimens examined have left spine bent somewhat near base.

Ceraclea (Athripsodina) riparia (Albarda)
(Fig. 88)

Leptocerus riparius Albarda, 1874: 231; holotype apparently not selected; 2 male syntypes in B. M. (N. H.), London; syntypes from Batavia and Germania.

Leptocerus riparius Albarda; Martynov, 1924: 116.

Ninth tergum with pair of small dimples. Superior appendages short, narrowed subapically. Tenth tergite slightly clavate in lateral view, its lateral processes long, relatively thick. Ventral lobe of coxopodite with two or three stout apical spines. Phallus large with anterior portion nearly twice as large as posterior apical portion. Ventral margin deeply excised in lateral aspect. Central Europe.

Ceraclea (Athripsodina) yangi (Mosely)
(Fig. 89)

Leptocerus yangi Mosely, 1942: 347; male; London; Foochow, China.

Ninth tergum with pair of small dimples. Superior appendages and tenth tergite similar to those of riparia. Ventral lobe of coxopodite with three apical spines not as stout as those of riparia. Phallus small, anterior and posterior ends of approximately equal size, and ventral margin not as strongly excised. Foochow, China.

Ceraclea (Athripsodina) modesta (Banks)
(Fig. 90)

Leptocerus modestus Banks, 1920: 350; male; Cambridge; Kapua near Tumbong, Hiang, Borneo.

Head and thorax fuscous with white setae. Forewings concolorous golden brown except white setae in band from vein 1A to hind margin and from wing base to arculus. Dark setal fringe apically. Superior appendages short, rounded, separated basally. Tenth tergite long, slightly clavate from the side, tapered from above. Lateral lobes of tenth tergite nearly as long as tergite, each with very large subapical, lateral spine. Ventral lobe of coxopodite with single large apical spine. Harpago flattened apically. Semimbranous anteriodorsal portion of phallobase greatly enlarged, extending cephalad far beyond phallic foramen (thin line on ventral margin in Fig. 90D). Left apical lateral lobe of phallobase with wide, rounded longitudinal groove. Right lateral lobe narrow. Borneo and Timor.

Lectotype. Nine syntypes are in the collection of the Harvard Museum of Comparative Zoology at Cambridge, Massachusetts. The first specimen of the series is a male bearing Banks' identification label and data, "Kapua near Tumbon, Hiang Borneo. 7.81. Grobowsky; Type 10890." This male is here designated the LECTOTYPE of Leptocerus modestus.

The lectotype and paralectotypes do not agree with Ulmer's (1951) figures, particularly in the shape of the tenth tergum. Apparently he had another species before him.

Ceraclea (Athripsodina) isurumuniya (Schmid)
(Fig. 91)

Leptocerus isurumuniya Schmid, 1958: 123; male; Schmid collection, Ottawa; Kitulgala, Ceylon.

Head and thorax fuscous with white and brown setae. Forewings uniformly fuscous. Ninth tergum narrow. Superior appendages very short, rounded, separated basally. Tenth tergite narrow and very long. Lateral lobes of tenth tergite also very long, slender, contiguous beneath main tergite apically, each with large apical spine surrounded by thin membrane. Ventral lobe of coxopodite with single apical spine. Harpago flattened, blade-like. Phallus very reduced with lateral parameres absent. Dorsal parameres apparently present, weakly sclerotized. Ceylon.

Ceraclea (Athripsodina) forcipata (Forsslund)
(Fig. 92)

Leptocerus forcipatus Forsslund, 1935: 9; male; Stockholm; Pe-lin-kou, Szechwan, China.

Superior appendages 1/2 as long as tenth tergite, fused basally. Tenth tergite upturned apically. Main body of inferior appendage slender, arched caudad. Ventral lobe of coxopodite originates baso-laterally, then curves posteriorly with huge apical and smaller subapical spines. Phallobase with large, bulbous anterior end. Left lateral apical lobe of phallobase narrower than right lobe. Szechwan, China.

Ceraclea (Athripsodina) flava (Banks)
(Fig. 93)

Leptocerus flavus Banks, 1904: 212; male; Cambridge; Falls Church, Virginia.
Athripsodes flavus (Banks); Ross, 1944: 228.

Superior appendages and tenth tergite similar to those of forcipata. Inferior appendage of same general shape as that of forcipata, but ventral lobe and apical spines smaller. Setose mesal ridge of coxopodite with rounded projection on caudal surface. Phallus similar to that of forcipata, but left apical lobe not sharply set off by subapical constriction; small, deep excision of ventral surface evident in lateral view. Central and eastern North America.

Ceraclea (Athripsodina) kamonis (Tsuda)
(Fig. 94)

Leptocerus kamonis Tsuda, 1942b: 290; holotype not selected; presumably at Nara; Kitaôji-bashi, Kamogawa, Kyoto, Japan.

Tenth tergite apparently without lateral processes. Main body of inferior appendage shaped as in forcipata and flava. Ventral lobe of coxopodite massive, relatively short, with single, very large, downcurved spine. Japan.

Ceraclea (Athripsodina) ancylus (Vorhies)
(Fig. 95)

Leptocerus ancylus Vorhies, 1909: 691; holotype not selected; syntype male at Cambridge; Dane County, Wisconsin.

Athripsodes ancylus (Vorhies); Ross, 1944: 227.

Superior appendages and tenth tergite similar to those of forcipata and flava. Main body of inferior appendage also of same general form as those species. Ventral lobe of coxopodite long, slender, with a single large apical spine. Phallobase with left apical lobe approximately same size as right and without deep ventral excision. Central and eastern North America.

Ceraclea (Athripsodina) neffi (Resh)

Athripsodes neffi Resh, 1974: 269; male; Urbana; Thoroughfare Gap, Broad Run, Bull Run Mountains, Fauquier Co., Virginia.

Similar in many respects to ancylus, but differing in that tenth tergite narrower in lateral view, with greatest width about 1/3 it length (greatest width about 1/2 its length in ancylus). Ventral aspect of ventral lobes of coxopodites angled posteriorly rather than curved mesad as in ancylus. Harpago of neffi shorter and broader. Kentucky and Virginia, North America.

Ceraclea (Athripsodina) nankingensis (Hwang)
(Fig. 96)

Leptocerus nankingensis Hwang, 1957: 389; male; Nanking; Nanking, Kiangsu, China.

Similar to ancylus but with superior appendages narrow subapically and tapered. Ventral lobe of coxopodite slender, downcurved apically, with single large apical spine. Kiangsu, China.

Marginata Group

Head and thorax light reddish-brown except in martynovi dark reddish fuscous. Forewings with light and medium brown setae in patches, especially along veins, forming irrorate pattern. Species marginata and martynovi have white setae in anal region of forewings and dark apical fringes similar to pattern in modesta. Main body of inferior appendage very reduced, semimbranous and inconspicuous in martynovi and marginata, absent in fooensis. Superior appendages long and tapered. Tenth tergite short, without lateral processes

Paramere spines retracted to same depth within phallobase, fused in fooensis.

Ceraclea (Athripsodina) fooensis (Mosely)
(Fig. 97)

Leptocerus fooensis Mosely, 1942: 348; male; London; Foochow, China.

Tenth tergite abruptly narrowed and nearly acute from above with pair of transverse, subapico-dorsal, sensilla-bearing ridges. Functional inferior appendage enlarged and recurved apically with apical crown of seta-bearing teeth. Mesal margin of coxopodite with four ridges: (a) ventral ridge with long setae, (b) longitudinal ridge with short, stout setae, (c) narrow, projecting, inconspicuous transverse ridge without setae, and (d) dorsal, longitudinal ridge without setae. Paramere spines fused. Phallobase long, without anterior bulbous development. Foochow, China.

Ceraclea (Athripsodina) martynovi (Forsslund)
(Fig. 98)

Leptocerus forcipatus Martynov, 1936: 253; male; presumably at Calcutta; Harra, Rewa State, India. Name preoccupied by Forsslund, 1935.

Leptocerus martynovi Forsslund, 1940: 48, new name.

Athripsodina martynovi (Forsslund); Kimmins, 1963: 278.

Hindwing with M vein unbranched. Superior appendages and tenth tergite acute from above, slender from side. Pair of low, rounded ridges near base of tenth tergite. Ventral lobe of coxopodite huge, bent mesad in rounded arch about midway and tapering to acute apex. Phallobase with bulbous anterior enlargement. Rewa, India.

Ceraclea (Athripsodina) marginata (Banks)
(Fig. 99)

Leptocerus marginatus Banks, 1911: 105; female; Cambridge; Pusa, Bengal, India.

Athripsodina marginata (Banks); Kimmins, 1963: 276.

Hindwing with M vein simple. Tenth tergite slightly clavate in lateral view, nearly truncate from above. Ventral lobe of coxopodite shorter than in two preceding species with bare subapico-ventral lobe, small crown of seta-bearing apical teeth, and angled baso-mesal, seta-bearing ridge. Phallobase small with slightly sclerotized phalicata lobes protruding from beneath semi-membranous apico-dorsal hood. Bengal, India.

Unplaced, Examined Species of Ceraclea (Athripsodina)

The following species can not be placed in any of the groups discussed above, nor have their phylogenetic relationships with those groups been ascertained. Rather than assign each species to a separate unassociated group, they are listed here for convenience pending a clearer understanding of their genealogic relationships.

Ceraclea (Athripsodina) dingwuschanella (Ulmer)
(Fig. 100)

Leptocerus dingwuschanellus Ulmer, 1932: 57; male; presumably at Hamburg; Dingwuschan, China.

Leptocerus dingwuschanellus Ulmer; Schmid, 1965: 147.

Head and thorax reddish fuscous with white and brown setae. Forewings

dark brown with gold-red to gold-yellow setae along posterior basal quarter, gold-yellow at arculus and a large patch of gold-yellow at apex. Superior appendages slender and rounded apically. Tenth tergite shorter with narrow apical excision, pair of subapical, transverse carina with sensilla, and without lateral processes. Coxopodite relatively simple, without ventral lobe. Harpago 1 1/2 times as long as semimembranous subapico-dorsal lobe of coxopodite. Lateral phallic paramere spines arranged as in Riparia Group except left (anterior) spine not bent. Dorsal parameres present, with left lobe apparently much longer; each lobe bears a short, sclerotized hook. Southeastern China.

This species may have arisen near the base of the lineage leading to the Riparia Group as is indicated by the derived arrangement of its paramere spines.

Ceraclea (Athripsodina) ensifera (Martynov)
(Fig. 101)

Leptocerus ensifer Martynov, 1935: 228; type sex and deposition unknown; River Lefu, near the lake Chanka, Amur, Siberia.

Head and thorax mostly light reddish-brown with white and light brown setae. Forewings with concolorous light reddish-brown setae except very small whitish mark at arculus. Sclerotization of ninth sternum discontinuous with narrow membranous strip dividing it all the way to the anterior margin; posterior ventral corners of sternum greatly elongate. Tenth tergite narrow, slightly clavate; lateral processes thick with subapical, dorsal triangular projection. Inferior appendages narrow from the side, each with long, saber-like phallic guide. Harpago long. Left paramere spine very reduced. Amur region, Siberia.

This species closely resembles kashingensis on several points. Its phallus has several derived character states in common with that of kolthoffi. The elongate, saber-like phallic guides of the coxopodites are reminiscent of those of variabilis.

Ceraclea (Athripsodina) kashingensis (Tsuda)
(Fig. 102)

Leptocerus kashingensis Tsuda, 1943: 105; type sex unknown; presumably at Nara; Kashing, Chekiang Prov., China.

Very similar to ensifera. Superior appendages more rounded apically from above. Tenth tergite narrower and lateral tenth tergal lobes narrower and curved mesad. Chekiang, China.

This species is closely related to ensifera as is indicated by the peculiar shape of the ninth sternum.

Ceraclea (Athripsodina) kolthoffi (Ulmer)
(Fig. 103)

Leptocerus kolthoffi Ulmer, 1932: 55; male; Stockholm; Kiangsu Prov., China.
Leptocerus inchinus Mosely, 1942: 347. NEW SYNONYM.

Head and thorax light reddish-brown with mostly white and few light brown setae. Forewings with short white and brown setae thoroughly intermixed except small white arculus and small brown region just beyond arculus. Superior appendages fused basally but acute and widely separated apically. Tenth tergite forming narrow hood, the lateral projections thick with short, transverse, subapical ridge. Inferior appendages narrow from side with mesal ridge protracted in dagger-like process. Harpago large. Left paramere

spine seta-like, deeply retracted. Left lateral lobe of phallobase narrower than right, subacute apically. Southeastern China.

This species is possibly a member of a small monophyletic group with ensifera, kashingensis, major, and variabilis. Each of these species bears one or more derived character states in common with one or two of the other species. However, each species has diverged very strongly such that it is difficult to specify their sequence of development or the position of the group in the evolutionary tree of the subgenus. On the basis of the arrangement of the paramere spines in ensifera and kolthoffi, however, it is possible that these species may be members or close relatives of the Annulicornis Group. The discovery of other related species would probably give considerable help in determining these relationships.

Ceraclea (Athripsodina) ungulifera (Kimmins)
(Fig. 107)

Athripsodes ungulifera Kimmins, 1963: 279; male; Stockholm; Kambaiti, 6700 ft., northeastern Burma.

Head and thorax dark reddish-fuscous. Wings uniform reddish-brown. Genitalia of male resemble those of Tarsipunctata Group in having long, well-separated lateral processes of tenth tergum. However, phallus without distinct phalicata, phallotremal sclerite deep within phallobase and peculiar third paramere spine present. Northeastern Burma.

Ceraclea (Athripsodina) variabilis (Martynov)
(Fig. 108)

Leptocerus variabilis Martynov, 1935: 225; type sex and deposition unknown; village Bikin, Bikin River (trib. of Ussuri), Amur, Siberia.

Thorax dark reddish-fuscous, head lighter, both with white setae. Forewings brown with dark brown setae in a large apical patch, and in smaller patches over the stigma and beyond the arculus. Otherwise long whitish setae give wings hoary appearance. Superior appendages short, divergent. Ninth tergum with a pair of dimples. Tenth tergite broad from above, without lateral processes. Inferior appendages narrow from the side, each with short, narrow ventral lobe and long, sinuate phallic guide. Phallic shield broad ventrally, not fused to bases of coxopodites. Phallobase short dorsally, lateral parameres subequal in size and retracted to about same depth, and dorsal parameres present as tiny sclerotized plates near the dorsal apex. Amur region, Siberia.

The phallic guides of the coxopodites of this species resemble those of ensifera. Its phallus is not very different in appearance from that of sibirica.

Ceraclea (Athripsodina) for which Adequate Study Material is Unavailable

Males of the following species were not available for comparative study. The descriptive literature is not adequate for the determination of their probable phylogenetic placement.

Ceraclea (Athripsodina) major (Hwang)
(Fig. 104)

Leptocerus major Hwang, 1957: 390; male; the Chinese Science College, Insect Research Institute; Yao Shan, Kwangsi Prov., China.

Close to variabilis according to Hwang, but tenth tergite slightly clavate from the side, narrower from above. Ventral lobe of coxopodite larger. Phallic guides broader. Harpago with two apical lobes widely divergent. Kwangsi, China.

Ceraclea (Athripsodina) mitis (Tsuda)
(Fig. 105)

Leptocerus mitis Tsuda, 1942b: 291; holotype not selected; presumably at Nara; Kitaôji-bashi, Kamogawa, Kyoto, Japan.

Male genitalia reminiscent of Annulicornis Group species. Readily distinguishable by broad ninth sternum and long lateral projections of ninth segment. Japan.

Ceraclea (Athripsodina) norfolki (Navás)

Leptocerus norfolki Navás, 1917c: 66; female; Zaragosa; Cercedilla, Spain.
Leptocerus norfolki Navás; Schmid, 1950: 368.

Genitalia of single female type resemble those of species in the Annulicornis Group. Specimen somewhat rubbed, but color not very different from that of aurea. Spain.

Ceraclea (Athripsodina) signaticornis (Ulmer)
(Fig. 106)

Leptocerus signaticornis Ulmer, 1926: 64; male; presumably in Mell collection in Canton; "Lotosteiche," Canton, Kwangtung Prov., China.

Probably a species of the Annulicornis Group, but superior appendages much longer and much more divergent from the base than other known species. Kwangtung, China.

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Fig. 1. Larval head of Erotesis baltaica. A, dorsal. B, ventral.

Fig. 2. Larval head of Athripsodes aterrimus. A, dorsal. B, ventral.

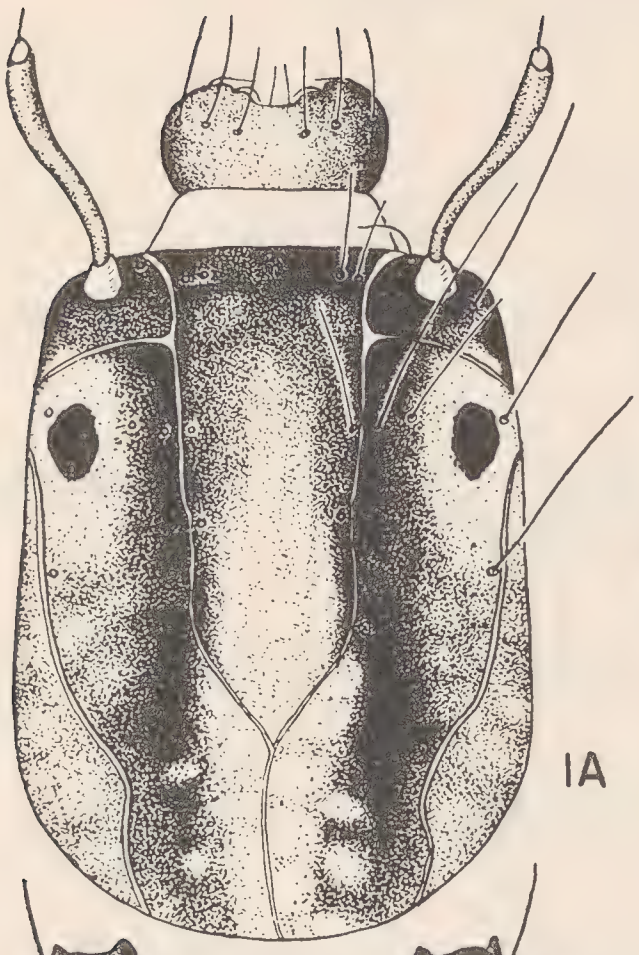
Fig. 3. Larval head of Ceraclea (Athripsodina) excisa. A, dorsal. B, ventral. C, left lateral.

Fig. 4. Larval mesonotum of Athripsodes cinereus.

Fig. 5. Larval mesonotum of Ceraclea (Athripsodina) excisa.

Fig. 6. Larval head of Ceraclea (C.) fulva, dorsal.

(all from Lepneva, 1966)



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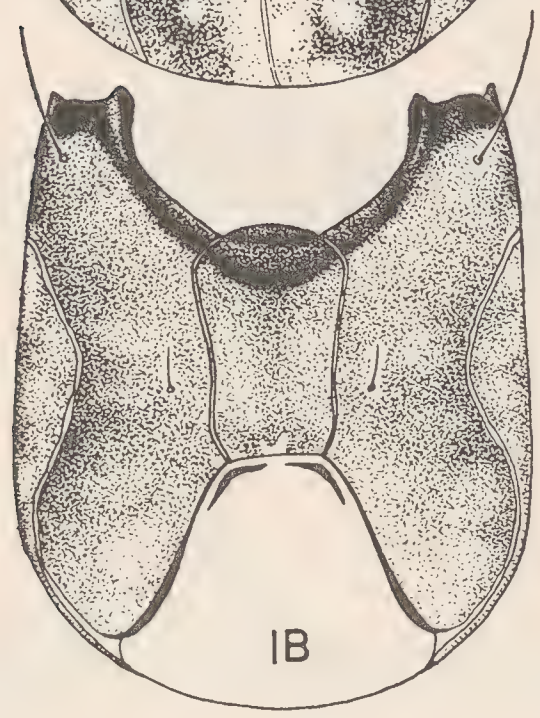

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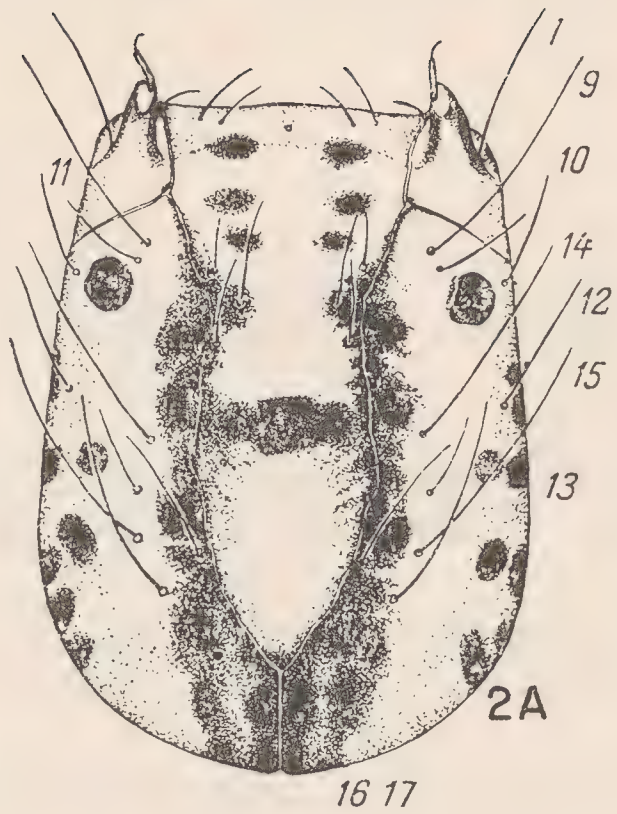

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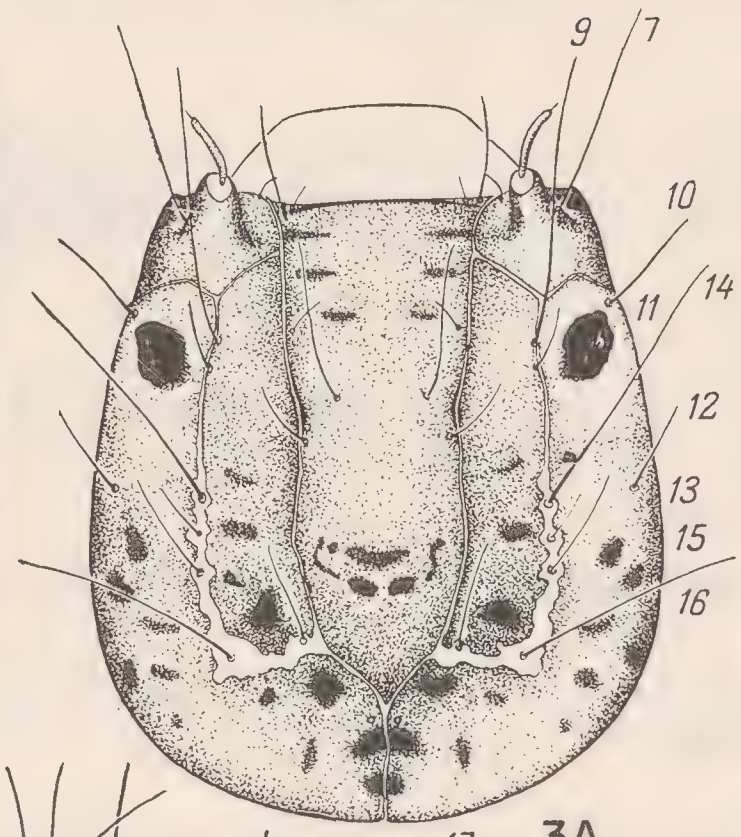

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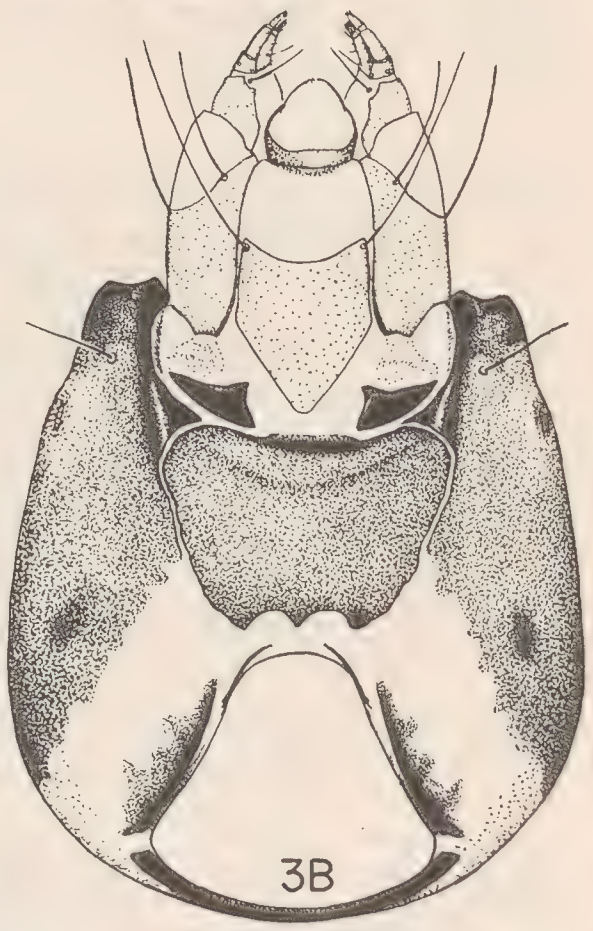

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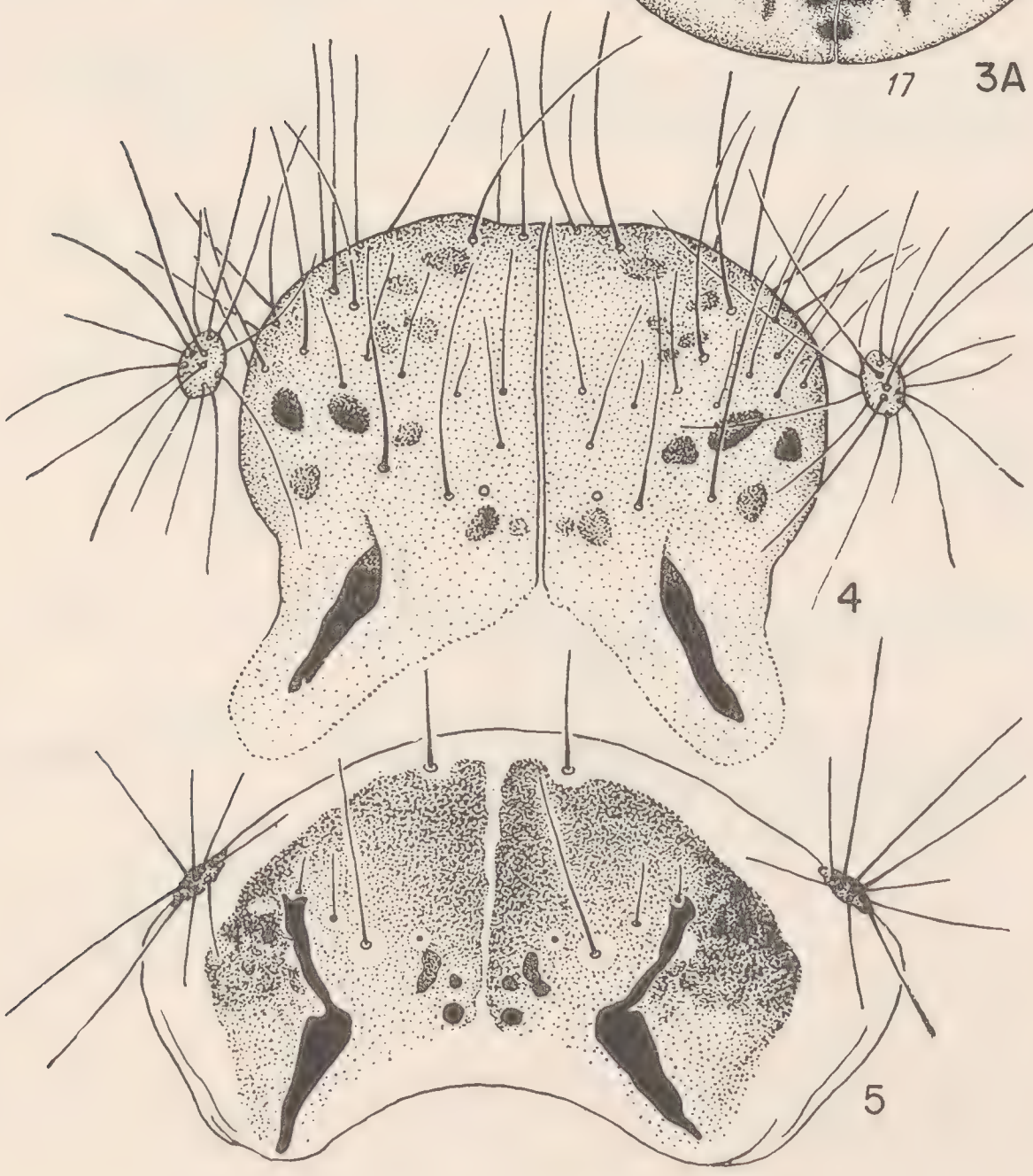

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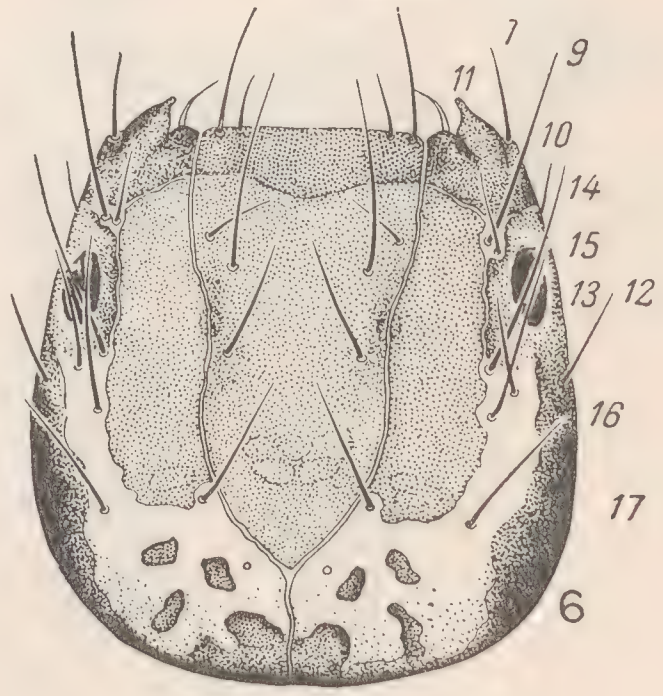

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Fig. 7. Larval case of Athripsodes bilineatus, left lateral. (redrawn from Hickin, 1967)

Fig. 8. Larval case of Ceraclea (Athripsodina) annulicornis. A, right lateral. B, ventral. C, dorsal. (from Lepneva, 1966)

Fig. 9. Apices of pupal antennae and abdomen of Mystacides longicornis. (from Lepneva, 1971)

Fig. 10. Pupal mandible of Ceraclea (Athripsodina) excisa. (from Lepneva, 1971)

Fig. 11. Lateral tubercle of first abdominal tergum of pupa of Ceraclea (Athripsodina) excisa. (from Lepneva, 1971)

Fig. 12. Pupal anal rods of Athripsodes aterrimus. (from Lepneva, 1971)

Fig. 13. Pupal anal rods of Ceraclea (Athripsodina) annulicornis. (from Lepneva, 1971)

Fig. 14. Adult Athripsodes bilineatus. (redrawn from Hickin, 1967)

Fig. 15. Adult pro- and mesonota of Ceraclea (Athripsodina) tarsipunctata. (from Ross, 1944)

Fig. 16. Adult right mesopleuron and coxa of Mystacides sepulchralis; em = epimeron, k = katepisternum. (from Ross, 1944)

Fig. 17. Adult right mesopleuron and coxa of Ceraclea (C.) transversa; em = epimeron, k = katepisternum. (from Ross, 1944)

Fig. 18. Female genitalia of Ceraclea (Athripsodina) dissimilis. A, left lateral. B, dorsal. C, ventral. D, detailed view of apex of ninth sternum and of internal bursal sclerite; rs = rounded sclerite. (from Kimmins, 1964)

Fig. 19. Female genitalia of Ceraclea (Athripsodina) tarsipunctata, ventral; rs = rounded sclerite. (from Ross, 1944)

Fig. 20. Female genitalia of Ceraclea (C.) cancellata, ventral. (from Ross, 1944)

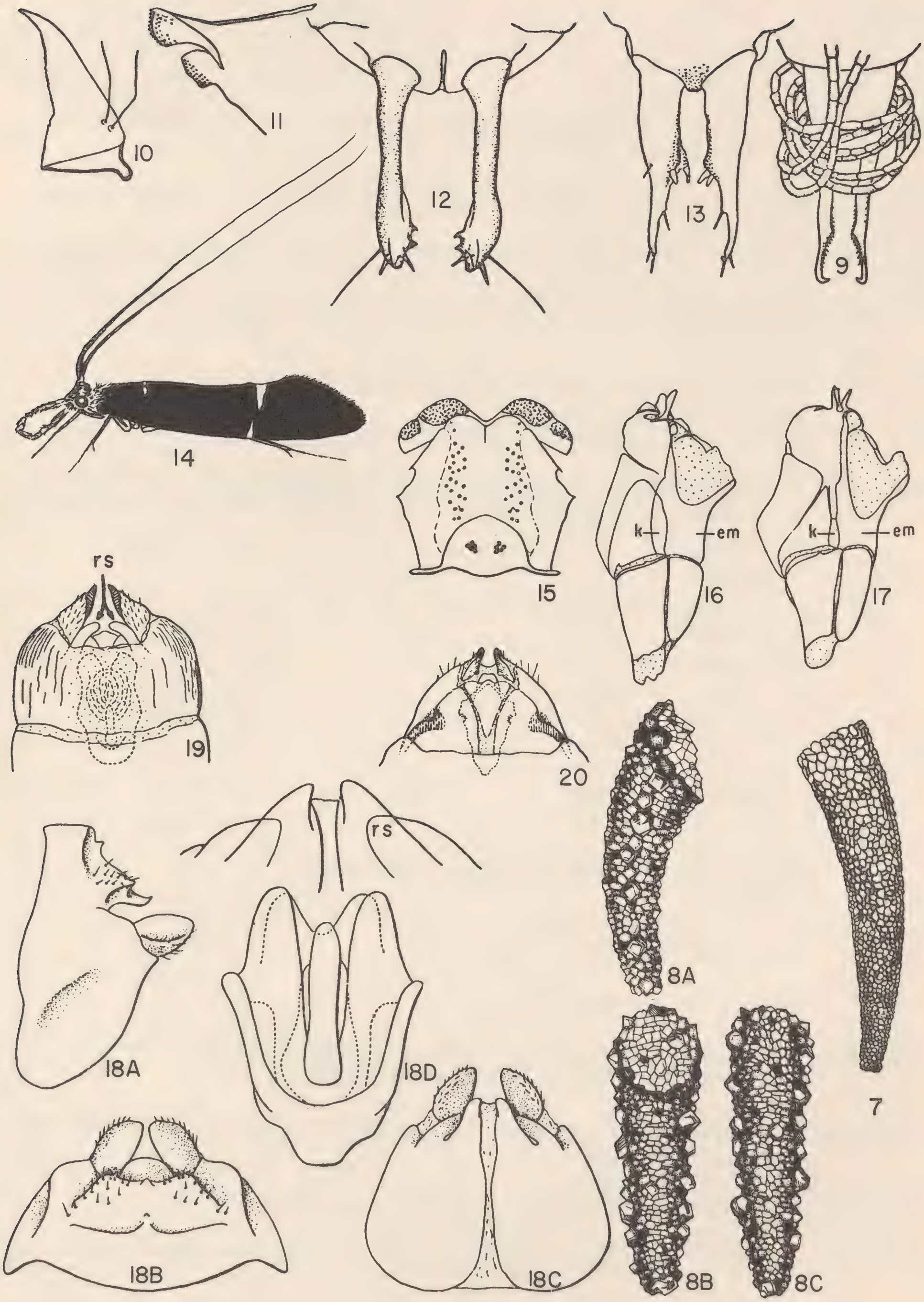

10
11
12
13
9
14
15
16
k
em
17
k
em
rs
19
20
rs
8A
18A
18D
18B
18C
8B
8C
7

Fig. 21. Adult head of Athripsodes aterrimus, dorsal; mcs = midcranial sulcus, ls = lateral sulcus.

Fig. 22. Adult head of Ceraclea (C.) transversa, dorsal; ls = lateral sulcus.

Fig. 23. Maxillary palp of adult Athripsodes cinereus, shown without setae.

Fig. 24. Maxillary palp of adult Ceraclea (C.) tarsipunctata, shown without setae.

Fig. 25. Left inferior appendage of male Athripsodes albifrons, lateral.

Fig. 26. Left inferior appendage of male Athripsodes aterrimus, lateral.

Fig. 27. Wings of male Ceraclea (Athripsodina) tarsipunctata. A, forewing. B, hindwing. Longitudinal veins (capitalized) indicated from anterior to posterior as follows:

C = Costa
SC = Subcosta
R = Radius
S = Sector
M = Media
Cu = Cubitus
P = Plical
E = Empusal
A = Anal
JB = Jugal bar

Crossveins (lower case) indicated as follows:

s = sectoral
m-cu = medio-cubital

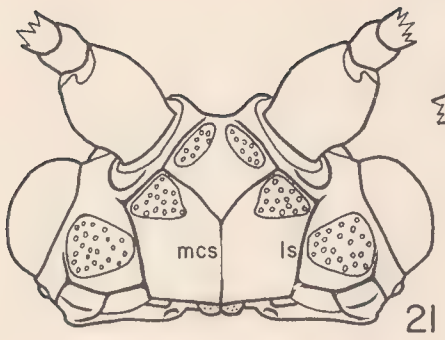
Also, "f. v." = false vein

Fig. 28. Wings of female Ceraclea (Pseudoleptocerus) sp. A, forewing. B, hindwing. Venational notation as in figure 27.

Fig. 29. Male genitalia of generalized Ceraclea species. A, left lateral. B, dorsal. C, caudal.

Fig. 30. Male genitalia of Athripsodes albifrons, dorsal.

Fig. 31. Phallus of generalized Ceraclea species. A, left lateral. B, dorsal.



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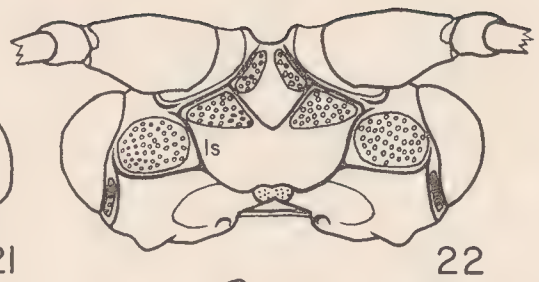

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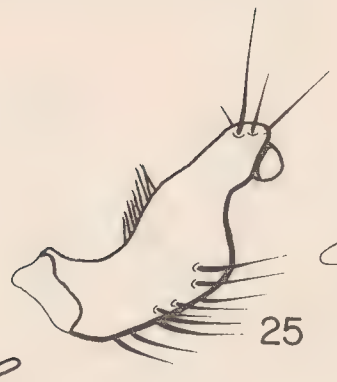
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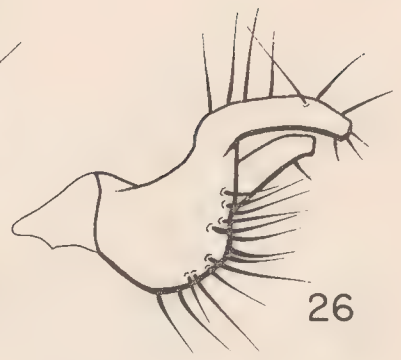
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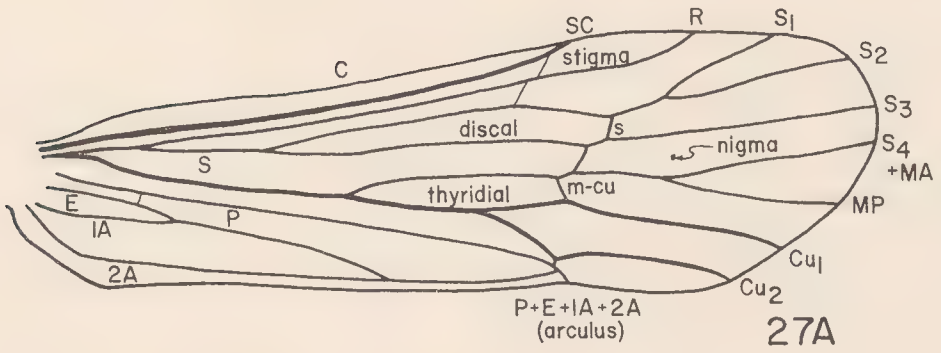

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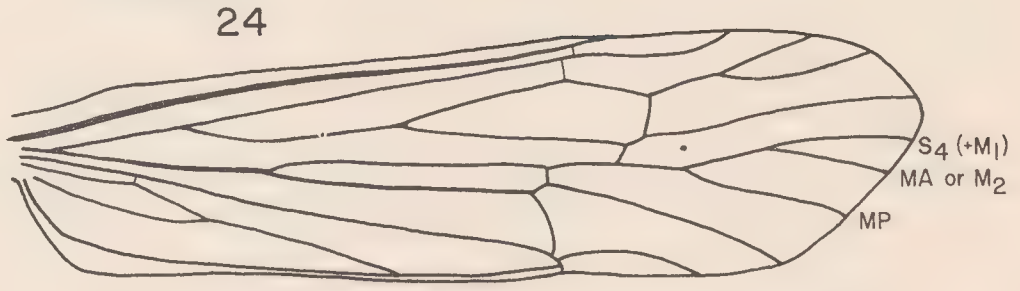

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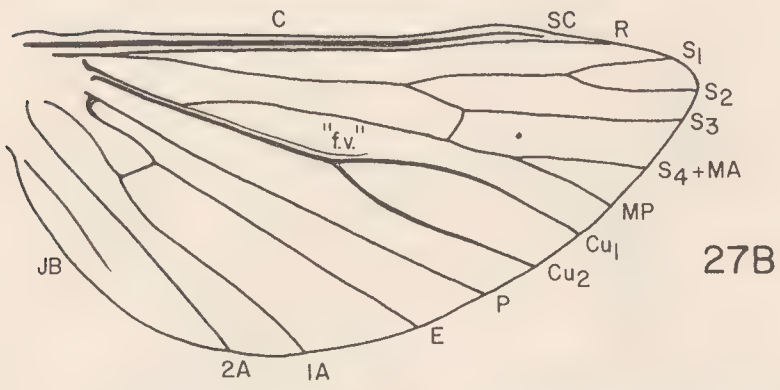

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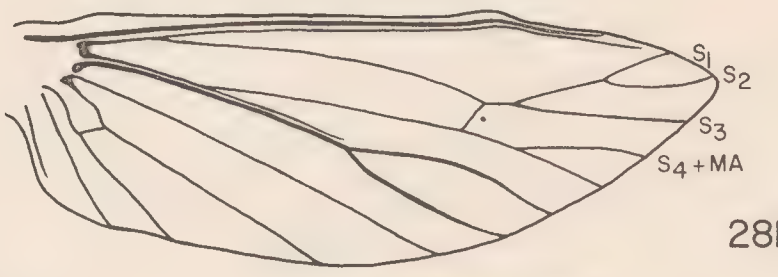

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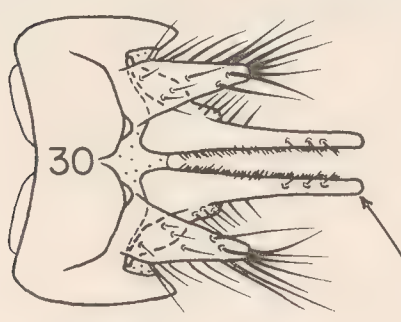
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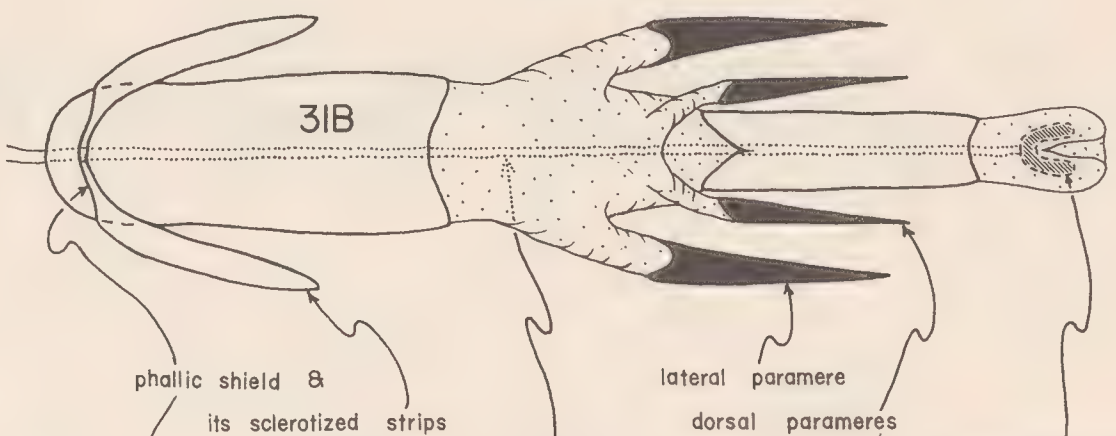
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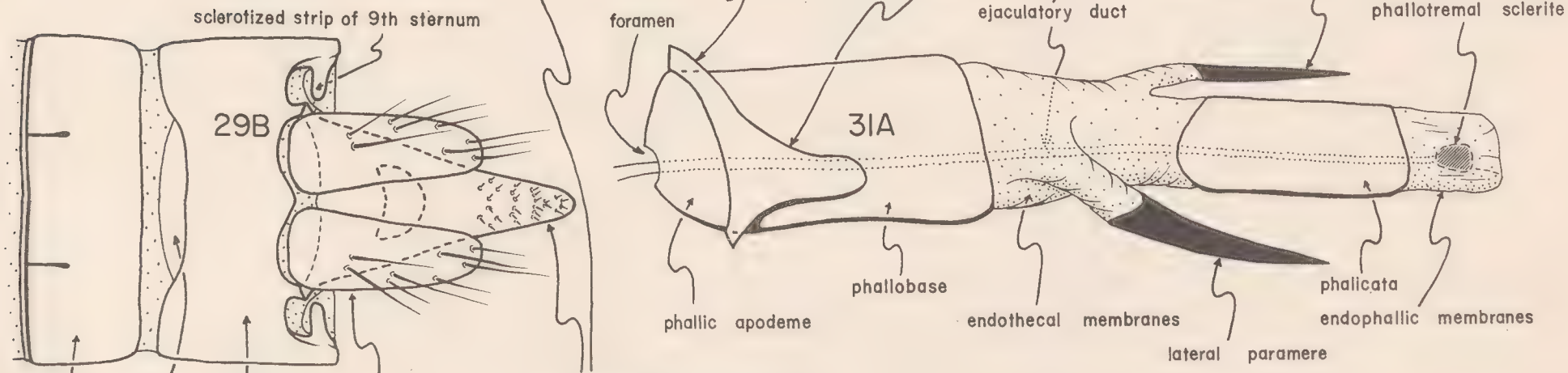


Fig. 32. Phylogeny of Ceraclea, its leptocerid ancestors, its subgenera, and its species groups. Developments of various characters discussed in text.

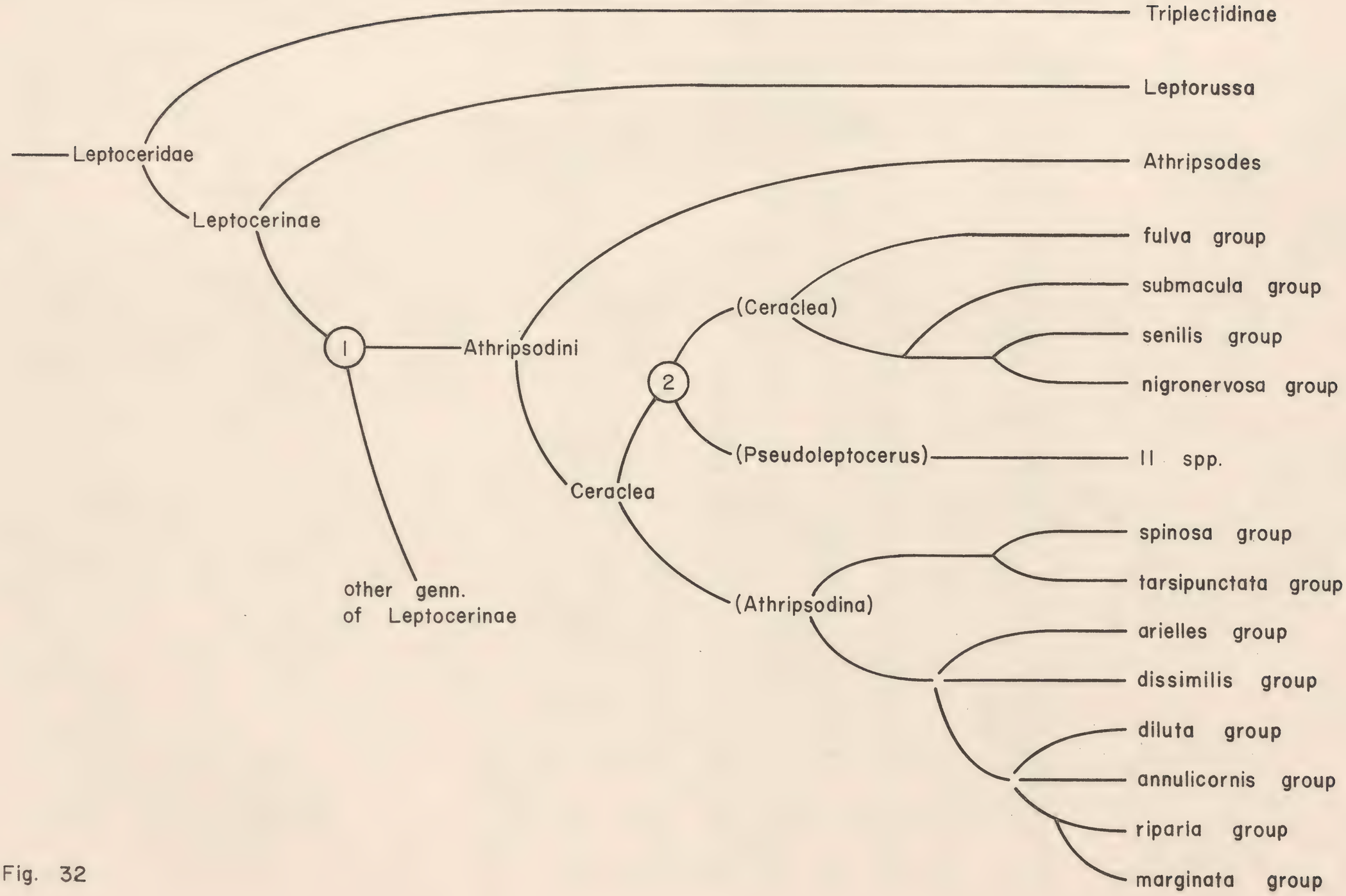

Triplectidinae
Leptorussa
Leptoceridae
Athripsodes
Leptocerinae
fulva group
submacula group
(Ceraclea)
1
Athripsodini
senilis group
2
nigronervosa group
(Pseudoleptocerus)
11 spp.
Ceraclea
spinosa group
tarsipunctata group
other genn.
of Leptocerinae
(Athripsodina)
arielles group
dissimilis group
diluta group
annulicornis group
riparia group
marginata group

Fig. 32

Figs. 33-39. Male genitalia of Ceraclea (C.) Fulva Group. A, left lateral. B, dorsal. C, inferior appendage, caudal. D, phallus, left lateral. E, apex of tenth tergite, caudo-ventral.

Fig. 33. Ceraclea (C.) cama (Flint), holotype.

Fig. 34. Ceraclea (C.) vertreesi (Denning), specimen from Oregon.

Fig. 35. Ceraclea (C.) biwaensis (Tsuda and Kuwayama). (from Tsuda, 1942, "Leptocerus spinosus")

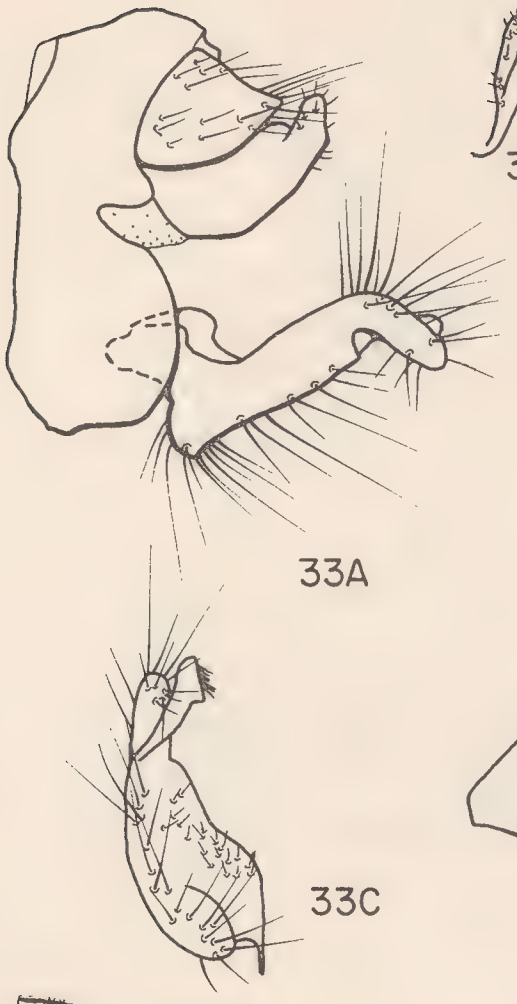
Fig. 36. Ceraclea (C.) resurgens (Walker), specimen from British Columbia.

Fig. 36'. Same, specimen from New York state.

Fig. 37. Ceraclea (C.) alces (Ross), holotype.

Fig. 38. Ceraclea (C.) alboguttata (Hagen), lectotype.

Fig. 39. Ceraclea (C.) transversa (Hagen), lectotype of Leptocerus angustus.



33A

33E

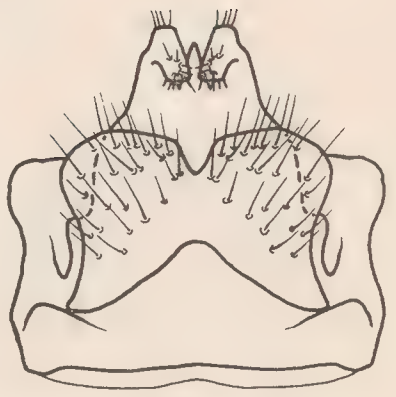
33B

33C

33D

34A

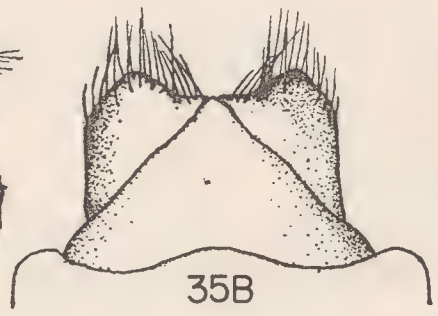
34E



34B

34D

35A



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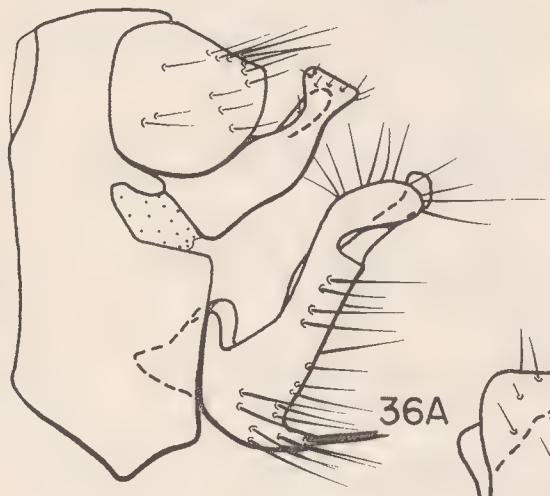
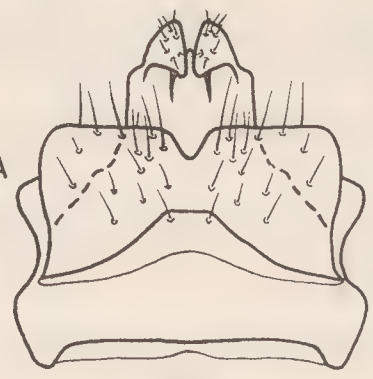


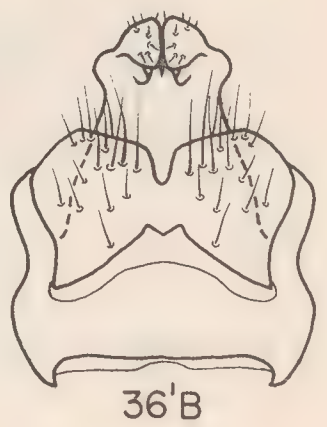
36A

36E



36B

36'E



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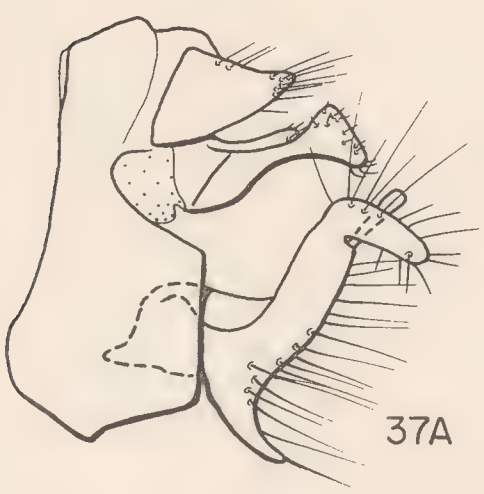

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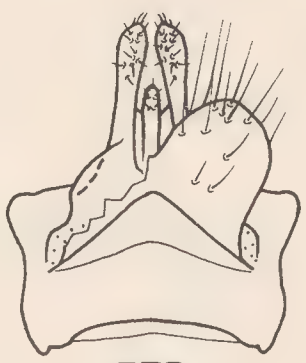

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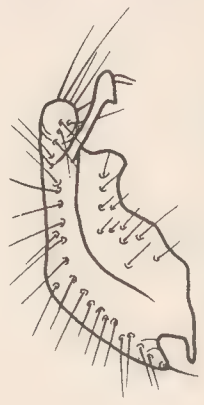

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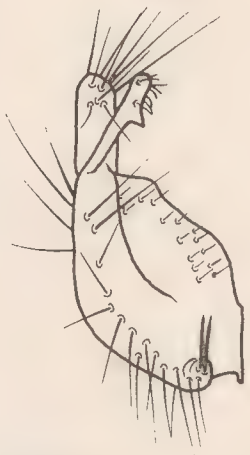

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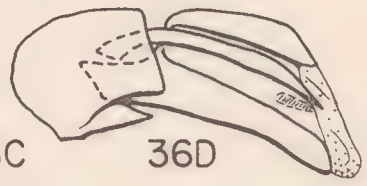

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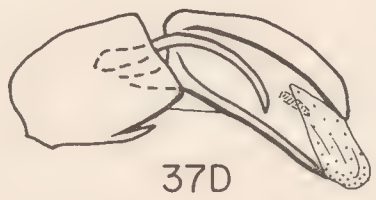
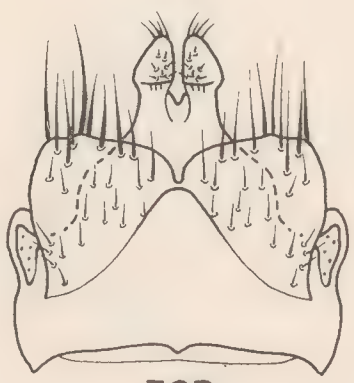


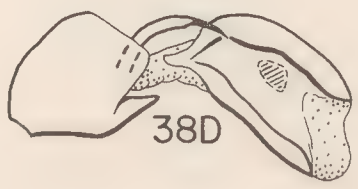
37D

38A



38B

38C



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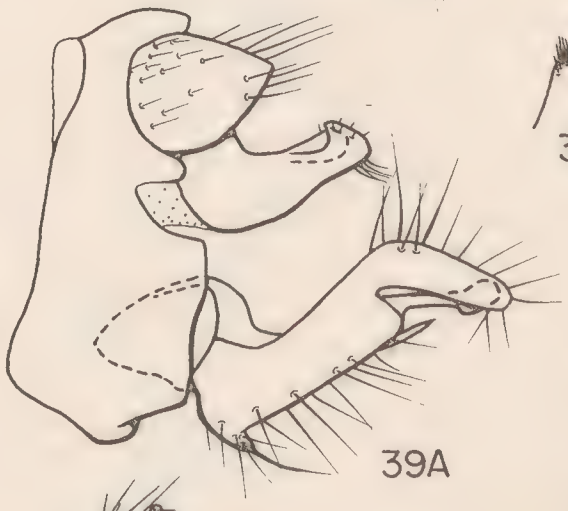
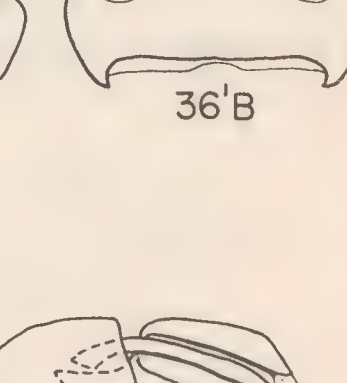


39A

39E



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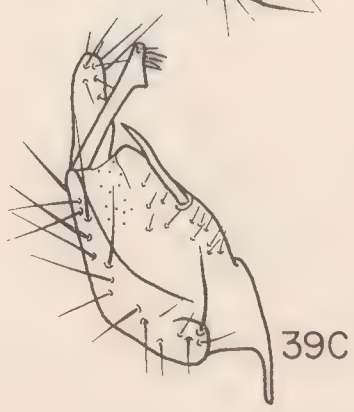

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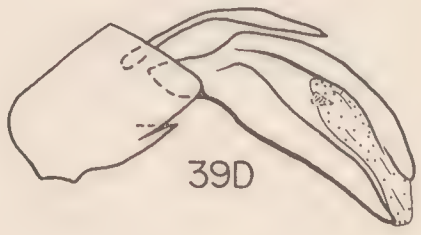


39D

Figs. 40-42. Male genitalia of Ceraclea (C.) Fulva Group; 43, Submacula Group; 44-45, Senilis Group. A, left lateral. B, dorsal. C, inferior appendage, caudal. D, phallus, left lateral. E, apex of tenth tergite, caudo-ventral.

Fig. 40. Ceraclea (C.) latahensis (Smith), holotype.

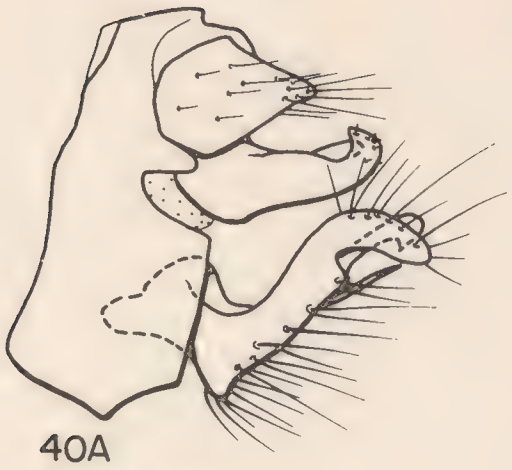
Fig. 41. Ceraclea (C.) fulva (Rambur), specimen from Switzerland.

Fig. 42. Ceraclea (C.) albimacula (Rambur), lectotype.

Fig. 43. Ceraclea (C.) submacula (Walker), specimen from Ohio.

Fig. 44. Ceraclea (C.) punctata (Banks), specimen from Maine.

Fig. 45. Ceraclea (C.) uvalo (Ross), holotype.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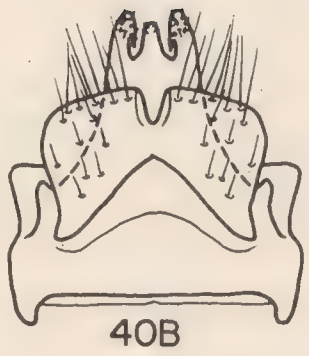
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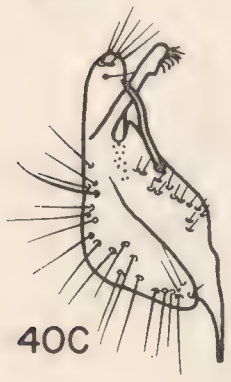
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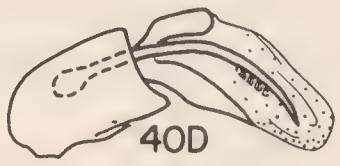
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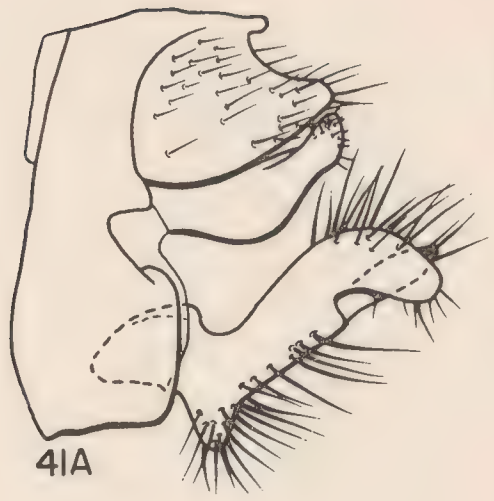
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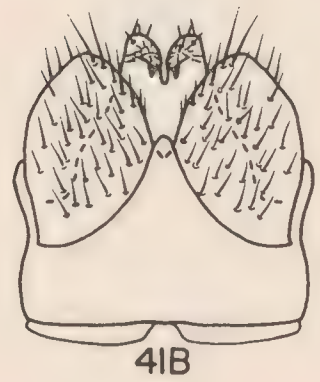
41E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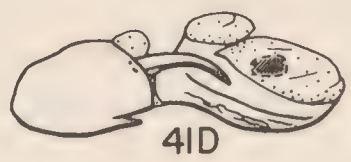
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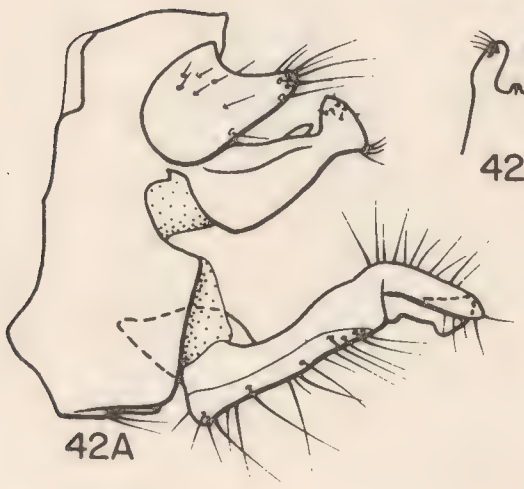
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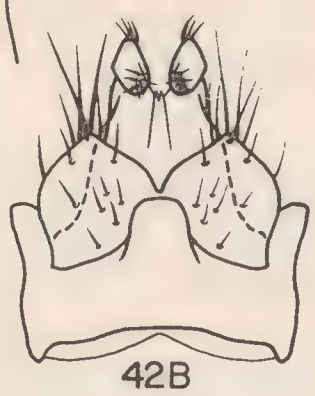
42E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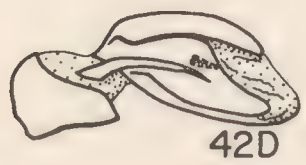
42C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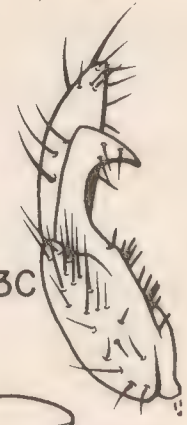
43A


43B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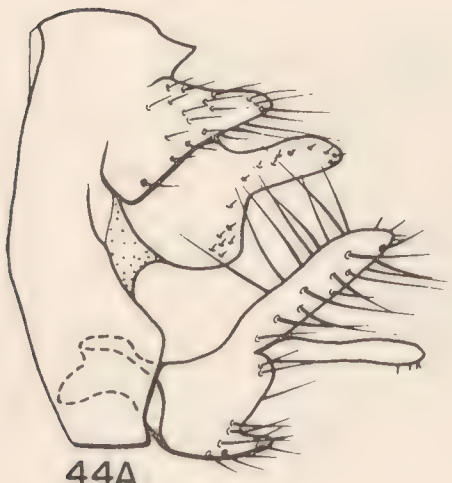
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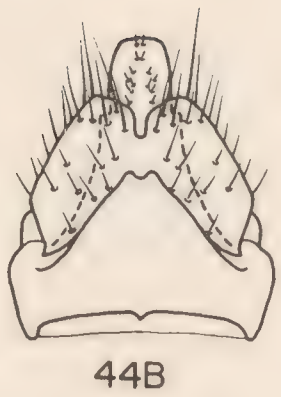
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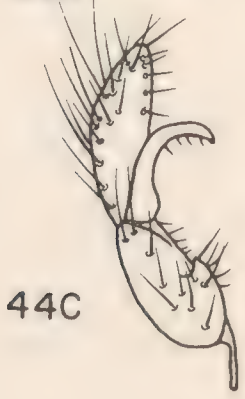
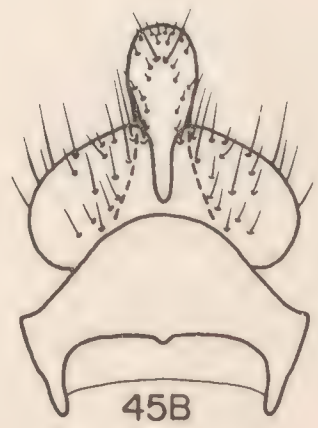

44C


44D


45A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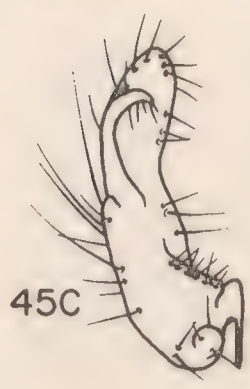

45C


45D

Figs. 46-48. Male genitalia of Ceraclea (C.) Senilis Group; 49-51, Nigronervosa Group. A, left lateral. B, dorsal. C, inferior appendage, caudal. D, phallus, left lateral.

Fig. 46. Ceraclea (C.) maculata (Banks), specimen from Georgia.

Fig. 47. Ceraclea (C.) senilis (Burmeister), specimen from France.

Fig. 48. Ceraclea (C.) cancellata (Betten), holotype. (Fig. 48D includes phallic shield covering much of phallobase)

Fig. 49. Ceraclea (C.) erulla (Ross), paratype.

Fig. 50. Ceraclea (C.) copha (Ross), holotype.

Fig. 51. Ceraclea (C.) ramburi Morse, new species, holotype.


46A

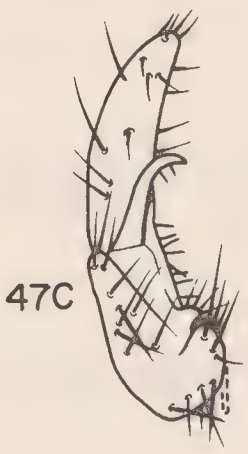

46B


47A


47B


46C


46D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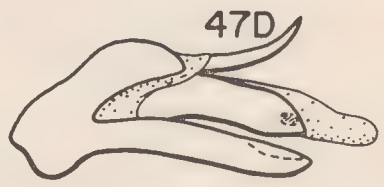
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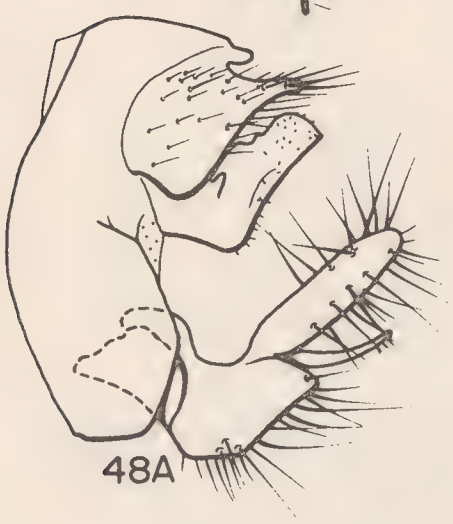
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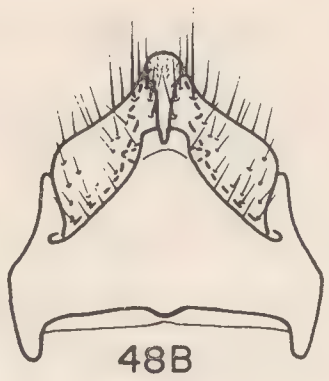
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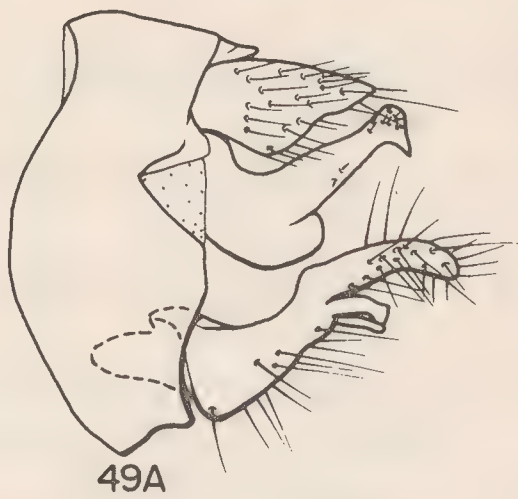
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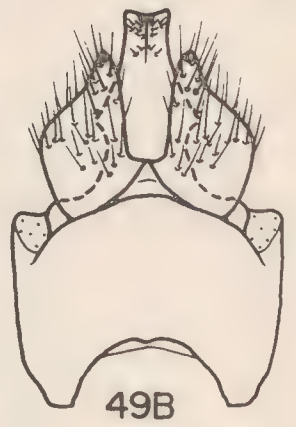
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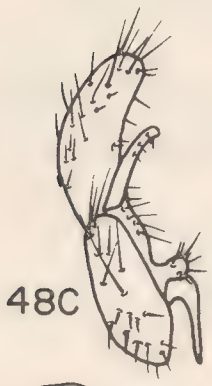
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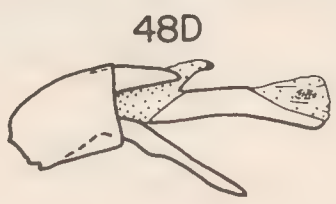
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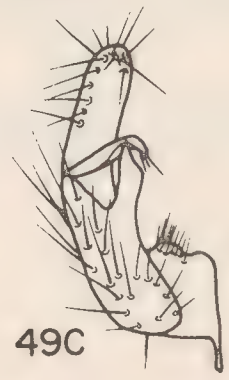
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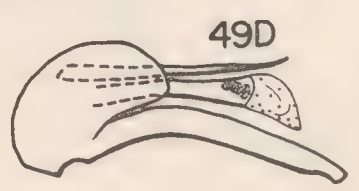
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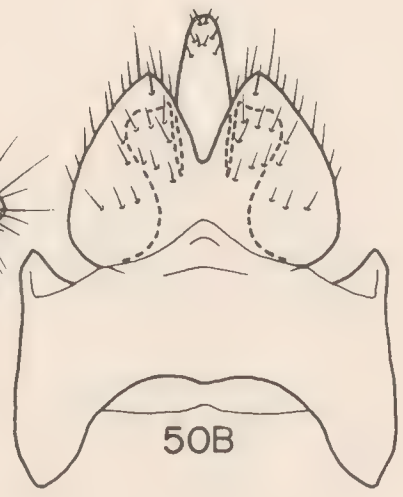
50A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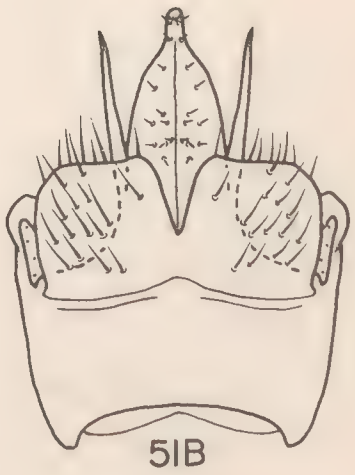
51A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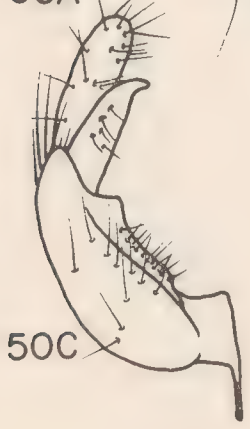
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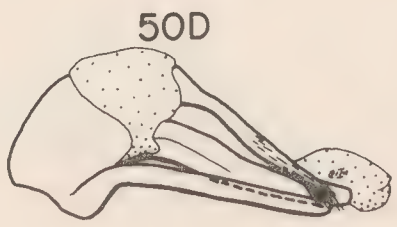
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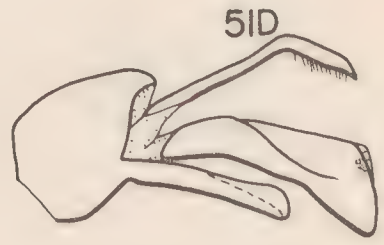

51D

Figs. 52-57. Male genitalia of Ceraclea (C.) Nigronervosa Group. A, left lateral. B, dorsal. C, inferior appendage, caudal. D, phallus, left lateral.

Fig. 52. Ceraclea (C.) nigronervosa (Retzius), specimen from Stephens collection.

Fig. 53. Ceraclea (C.) erratica (Milne), specimen from Quebec.

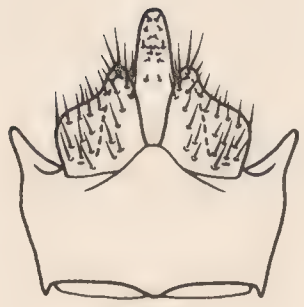
Fig. 54. Ceraclea (C.) albosticta (Hagen), specimen from Ohio.

Fig. 55. Ceraclea (C.) mentiea (Walker), specimen from New York state.

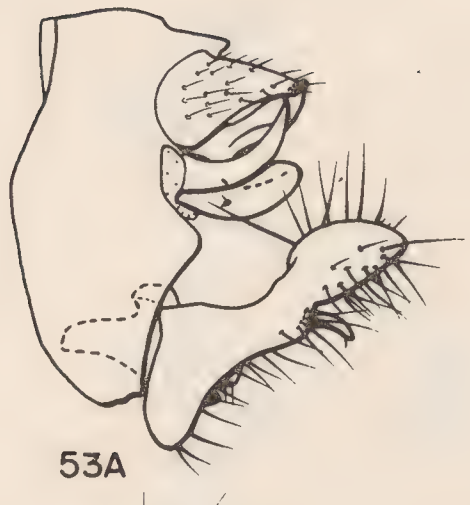
Fig. 56. Ceraclea (C.) slossonae (Banks); A, holotype of Athripsodes daggyi; B and C, specimen from Pennsylvania; D, specimen from Georgia, with inset of phallic paramere of specimen from West Virginia.

Fig. 57. Ceraclea (C.) ophioderus (Ross); A, B, and C of paratype; D, specimen from same locality in Georgia as specimen figured in 56D.

52A



52B



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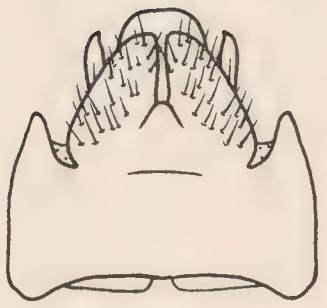

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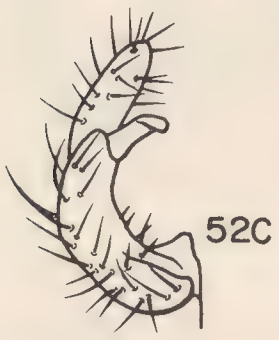
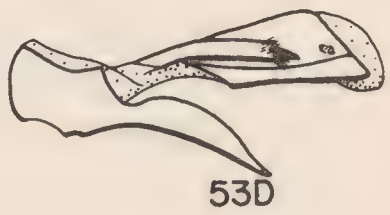


52C

52D

53C



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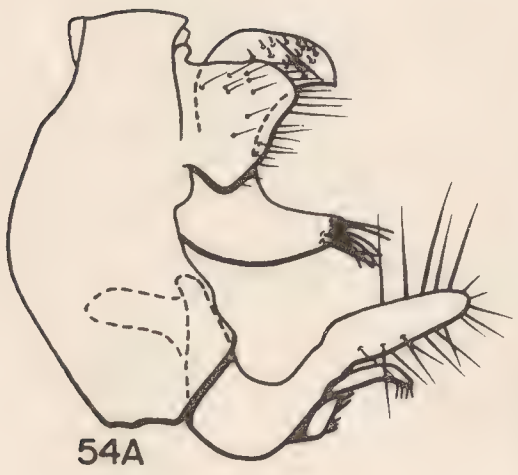
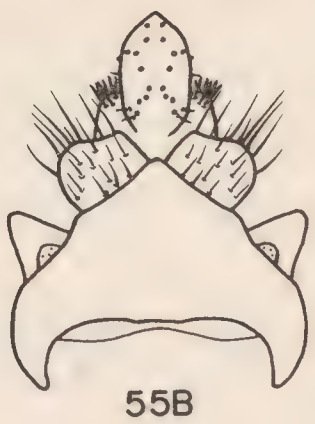


54A

54B

55A



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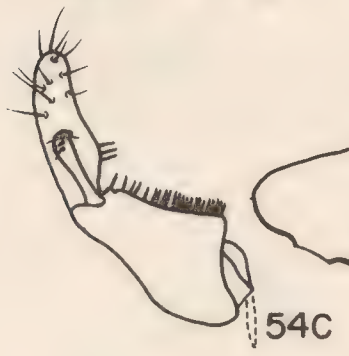

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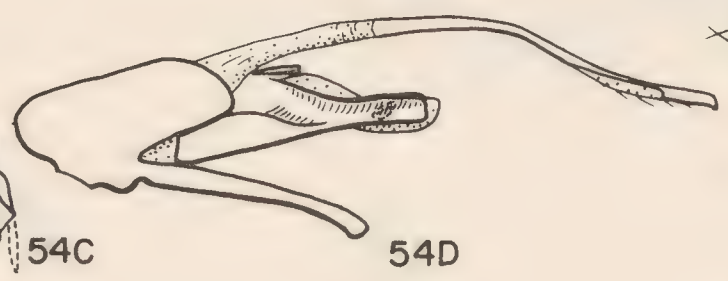
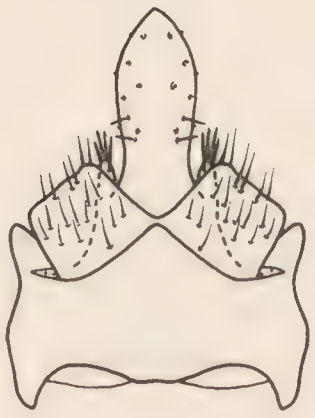


54D

55C

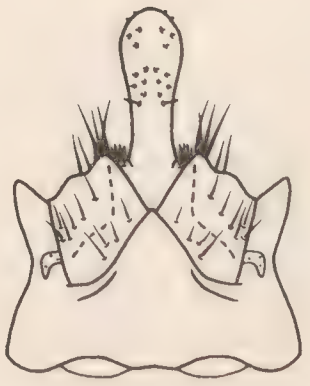
55D

56A

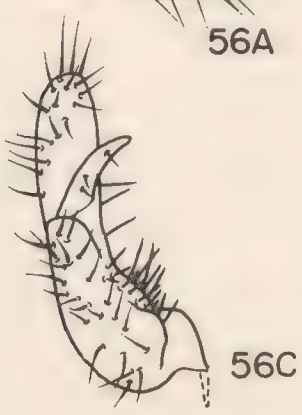


56B

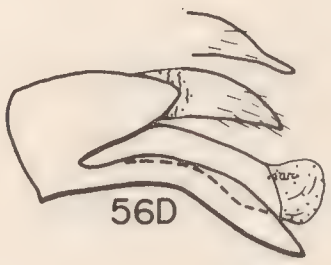
57A



57B

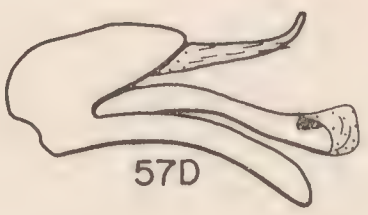


56C



56D

57C



57D

Figs. 58-59. Male genitalia of Ceraclea (C.) unexamined species; 60-62, Ceraclea (Pseudoleptocerus) species; 63, Ceraclea (Athripsodina) Spinosa Group. A, left lateral. B, dorsal. C, inferior appendage(s), caudal. D, phallus, left lateral. E, separate sclerite of ninth sternum.

Fig. 58. Ceraclea (C.) distinguenda (Martynov). (from Martynov, 1936)

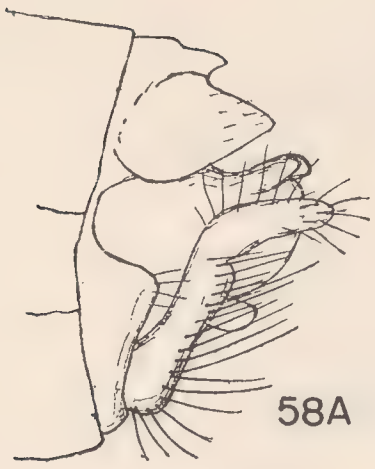
Fig. 59. Ceraclea (C.) superba (Tsuda). (from Tsuda, 1942b)

Fig. 60. Ceraclea (Pseudoleptocerus) minima (Kimmins), holotype.

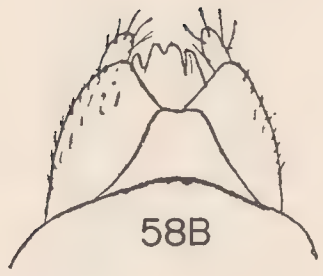
Fig. 61. Ceraclea (Pseudoleptocerus) schoutedeni (Navás), paratype.

Fig. 62. Ceraclea (Pseudoleptocerus) corbeti (Kimmins), specimen from Ghibe R., Ethiopia.

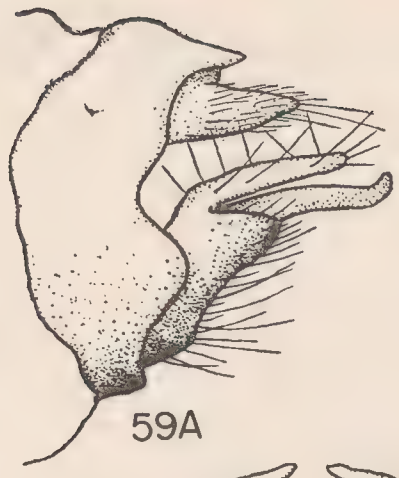
Fig. 63. Ceraclea (Athripsodina) microbatia (Marlier), paratype. (Fig. 63D includes phallic shield)



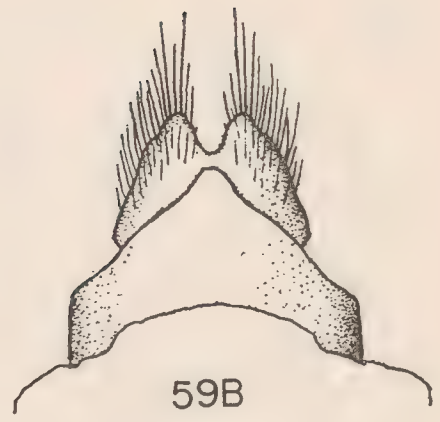
58A



58B



59A



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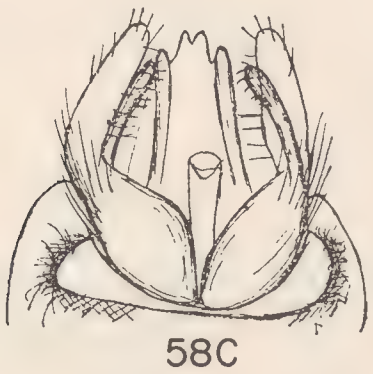

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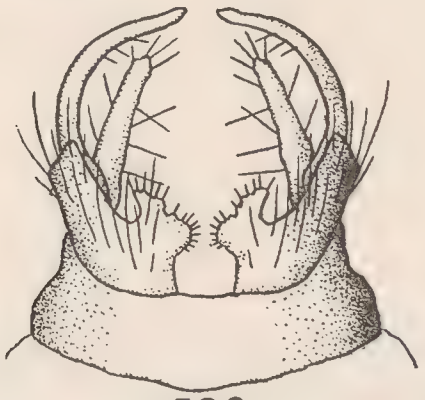
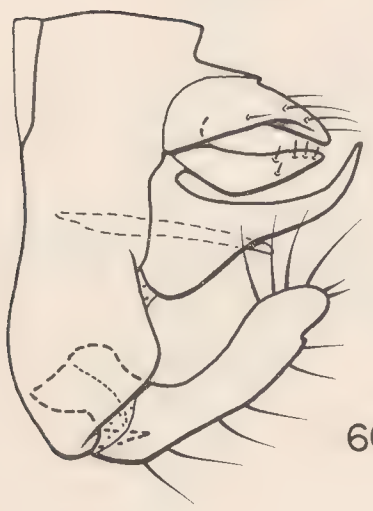
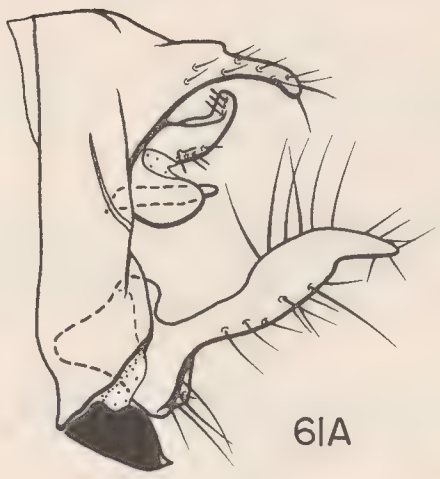


59C

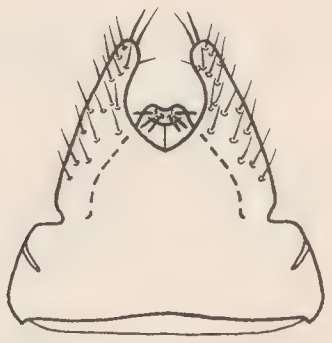


60A

60B



61A



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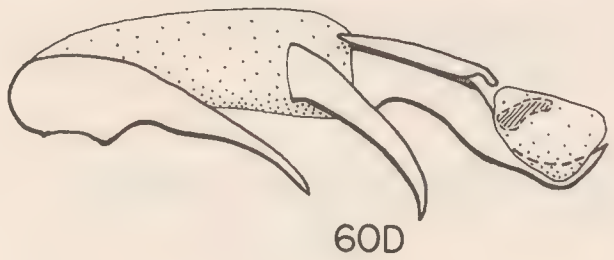
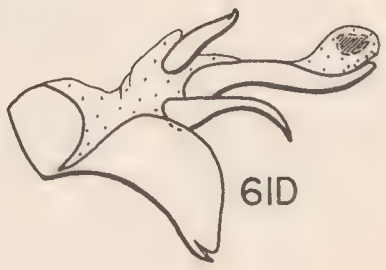


60D

61C

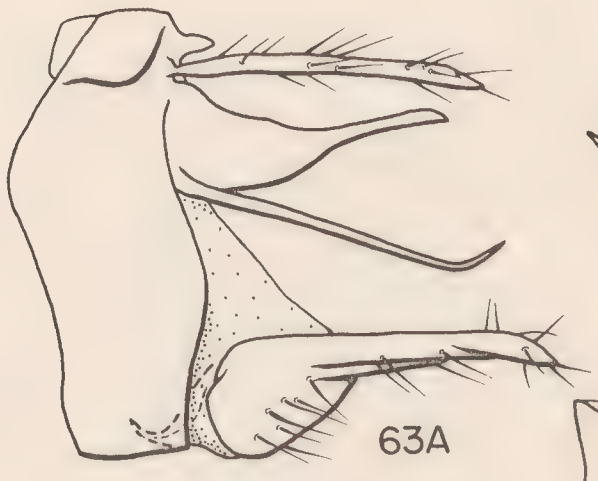
61E



61D

62A

62B

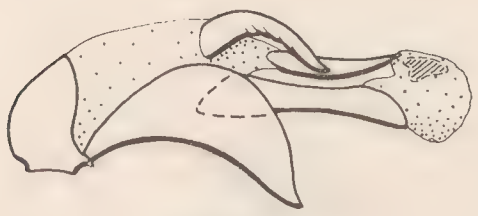


63A

63B

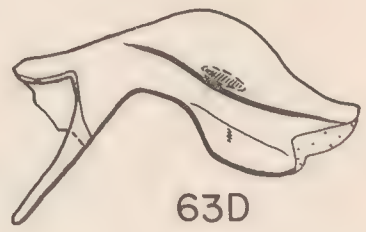
62E

62C



62D

63C



63D

Figs. 64-65. Male genitalia of Ceraclea (Athripsodina) Spinosa Group; 66-69, Tarsipunctata Group. A, left lateral. B, dorsal. C, inferior appendage, caudal. D, phallus, left lateral.

Fig. 64. Ceraclea (Athripsodina) batia (Mosely), holotype. (Fig. 64D includes phallic shield)

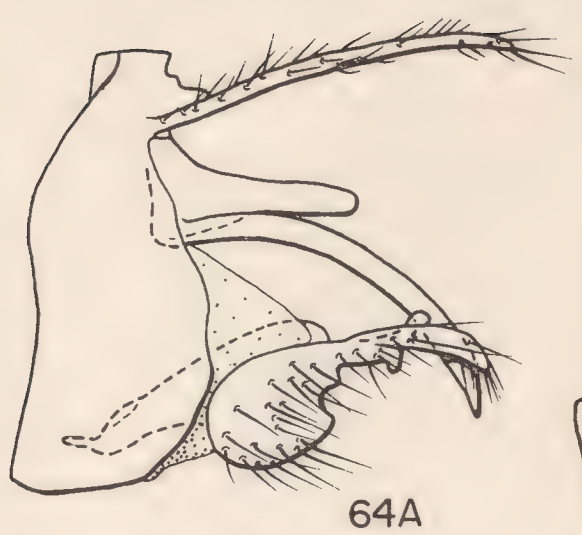
Fig. 65. Ceraclea (Athripsodina) spinosa (Navás), holotype. (Fig. 65A shows proximal end of phallobase with phallic shield in situ)

Fig. 66. Ceraclea (Athripsodina) brevis (Etnier), holotype.

Fig. 67. Ceraclea (Athripsodina) alagma (Ross), holotype.

Fig. 68. Ceraclea (Athripsodina) tarsipunctata (Vorhies); A, B, and D, specimen from Wisconsin; C, syntype.

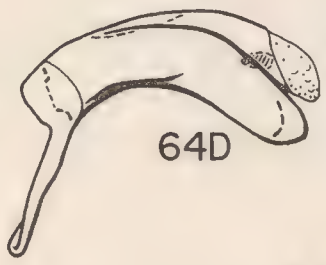
Fig. 69. Ceraclea (Athripsodina) nepha (Ross), holotype.



64A

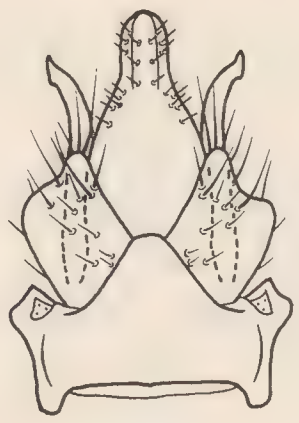
64B

64C

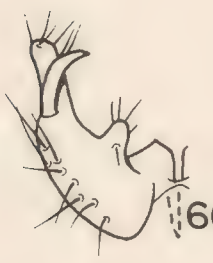


64D

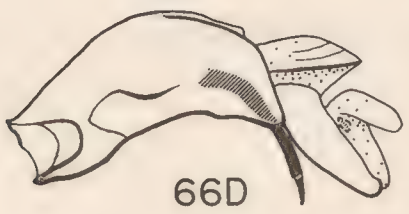
66A



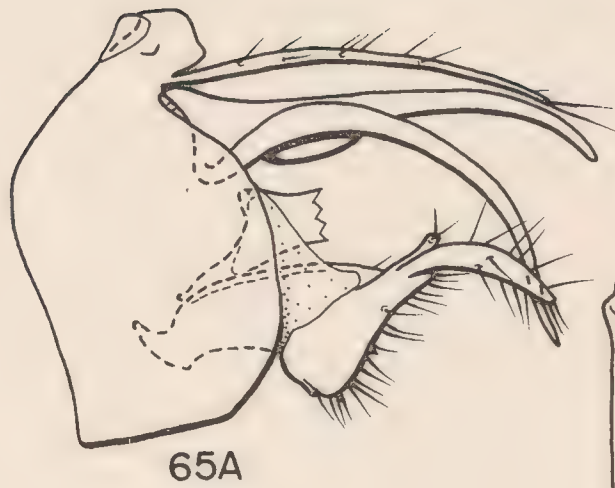
66B



66C



66D



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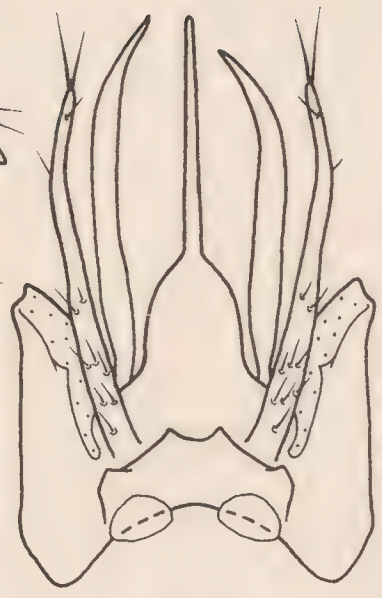
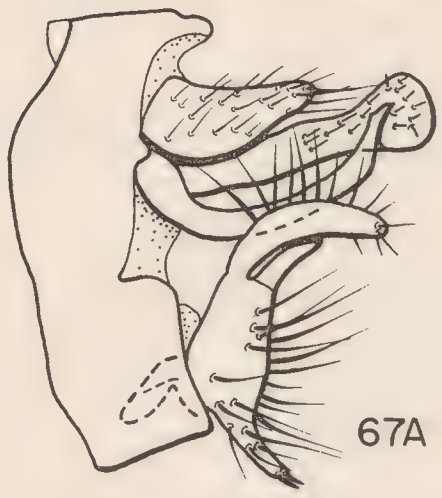


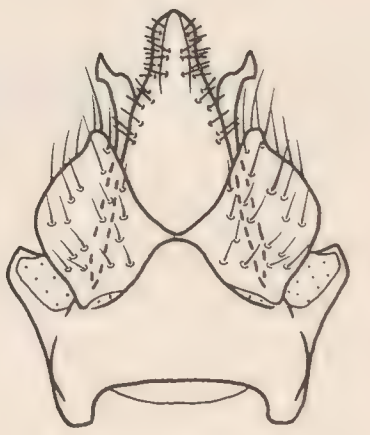
65B

65C

65D

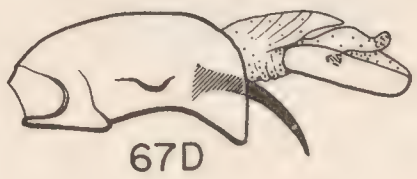


67A

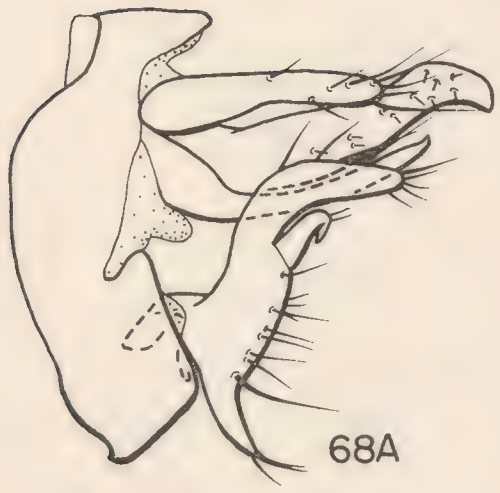


67B

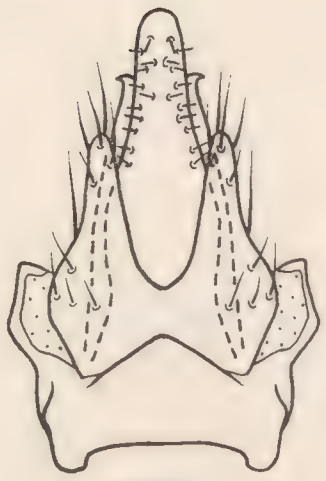
67C



67D

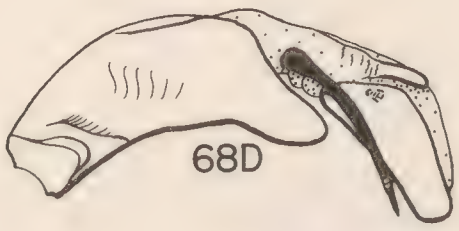


68A

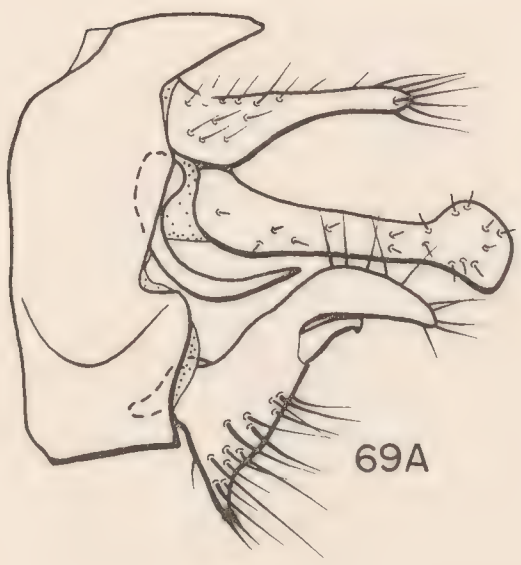


68B

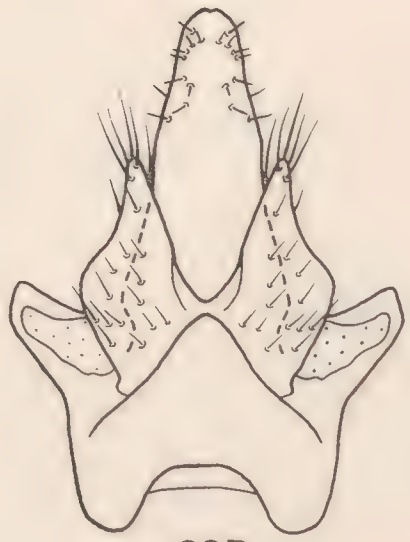
68C



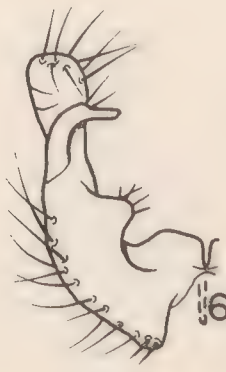
68D



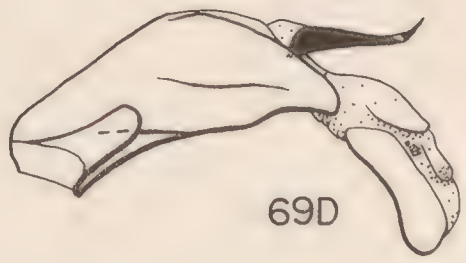
69A



69B



69C



69D

Fig. 70. Male genitalia of Ceraclea (Athripsodina) Tarsipunctata Group; 71, Arielles Group; 72-75, Dissimilis Group. A, left lateral. B, dorsal. C, inferior appendage, caudal. D, phallus, left lateral. E, phallus with endothecal membranes, parameres, and phalicata extruded, left lateral. F, same, ventral.

Fig. 70. Ceraclea (Athripsodina) protonepha Morse and Ross, new species, holotype.

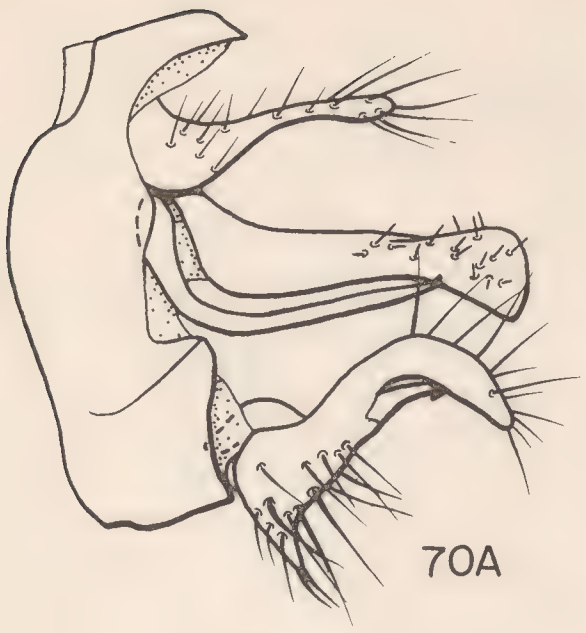
Fig. 71. Ceraclea (Athripsodina) arielles (Denning), specimen from Michigan.

Fig. 72. Ceraclea (Athripsodina) wetzeli (Ross), holotype.

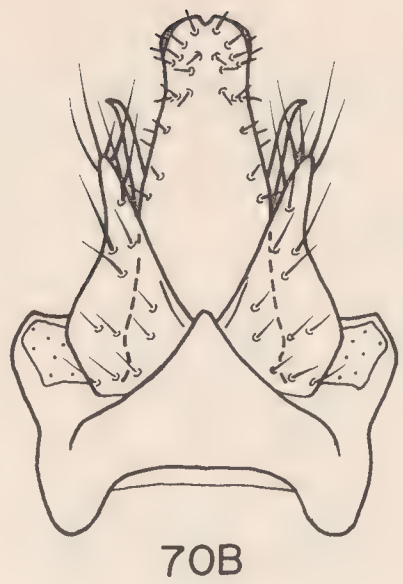
Fig. 73. Ceraclea (Athripsodina) miyakonis (Tsuda). (from Tsuda, 1942b)

Fig. 74. Ceraclea (Athripsodina) sobradieli (Navás), holotype.

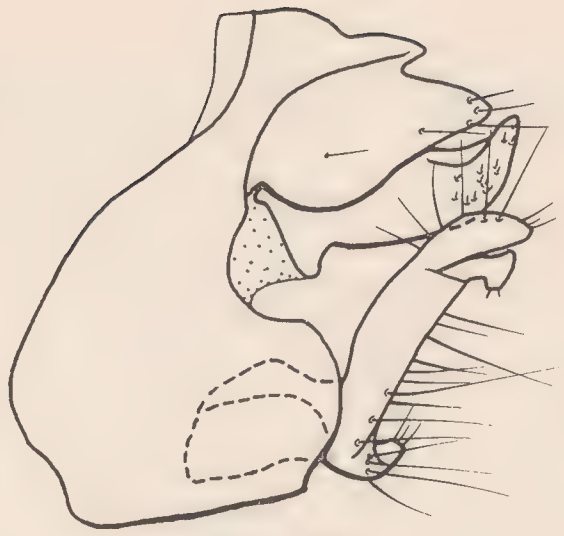
Fig. 75. Ceraclea (Athripsodina) dissimilis (Stephens), lectotype.



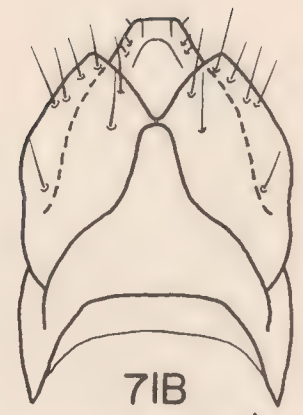
70A



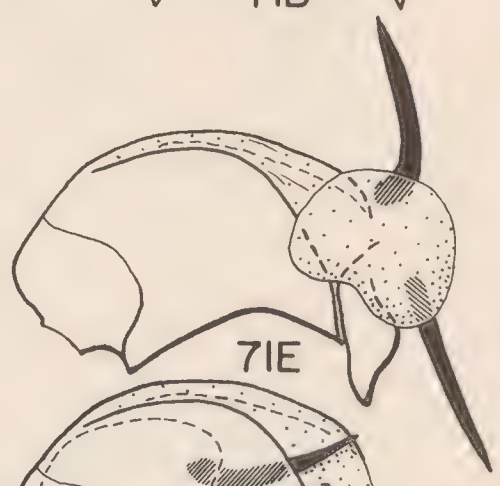
70B



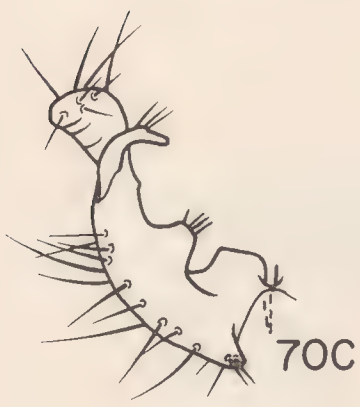
71A



71B

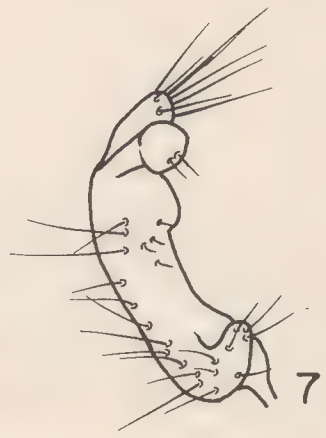


71E

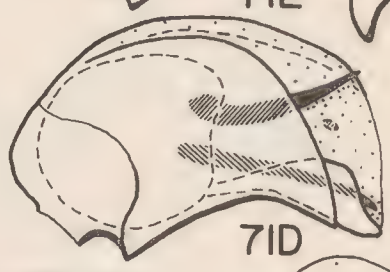


70C

70D

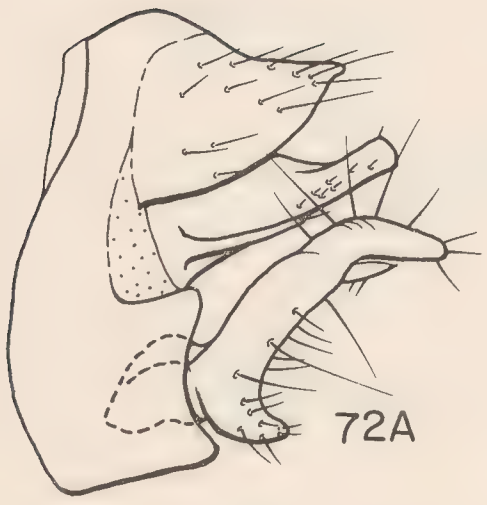


71C

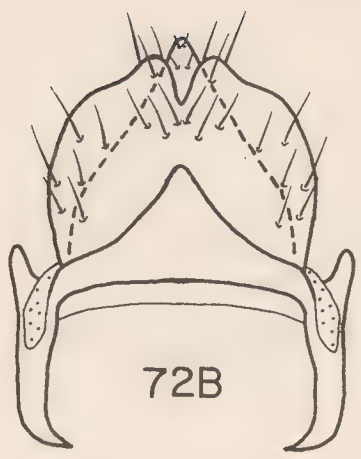


71D

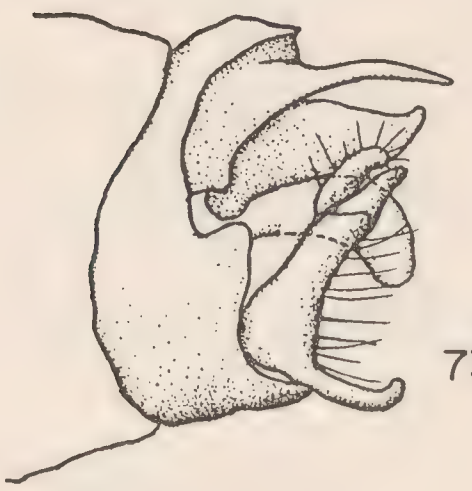
71F



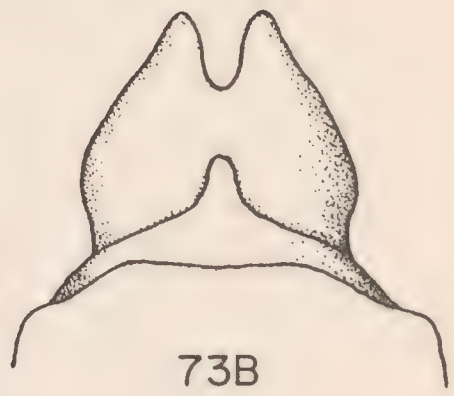
72A



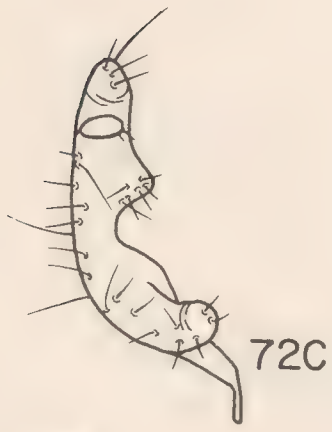
72B



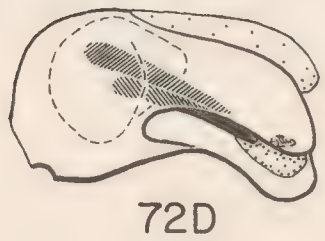
73A



73B



72C



72D

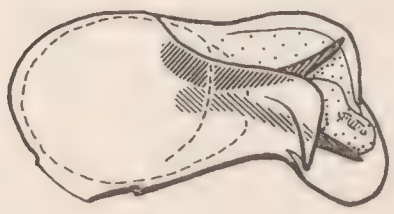
74A

74B

75A

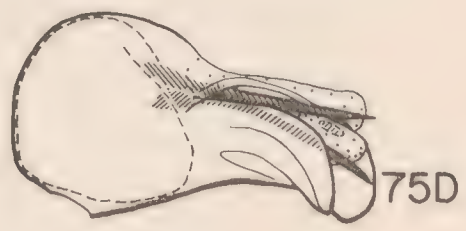
75B

74C



74D

75C



75D

Figs. 76-77. Male genitalia of Ceraclea (Athripsodina) Dissimilis Group; 78-79, Diluta Group; 80-82, Annulicornis Group. A, lateral. B, dorsal. C, inferior appendage(s), caudal. D, phallus, left lateral. E, same, ventral. F, ventral process of coxopodite, two lightly different positions.

Fig. 76. Ceraclea (Athripsodina) indistincta (Forsslund). (from Forsslund, 1935)

Fig. 77. Ceraclea (Athripsodina) lobulata (Martynov), paratype.

Fig. 78. Ceraclea (Athripsodina) diluta (Hagen), paratype.

Fig. 79. Ceraclea (Athripsodina) perplexa (MacLachlan), specimen from Iammela.

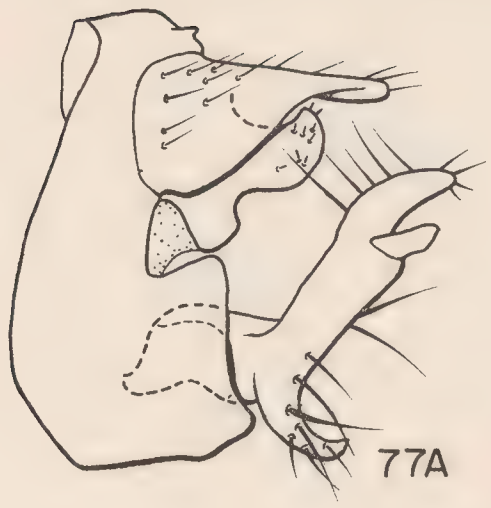
Fig. 80. Ceraclea (Athripsodina) aurea (Pictet), specimen from Kachalova.

Fig. 81. Ceraclea (Athripsodina) sibirica (Ulmer), lectotype.

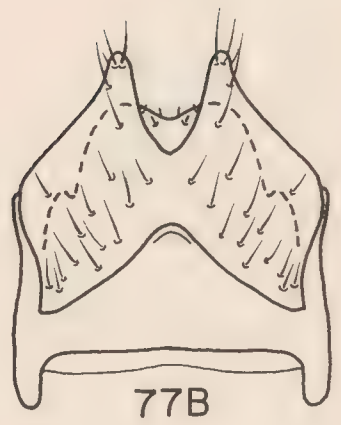
Fig. 82. Ceraclea (Athripsodina) hastata (Botosaneanu). (from Botosaneanu, 1970).

76A

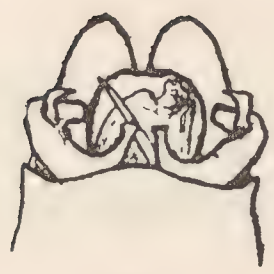
76B



77A



77B

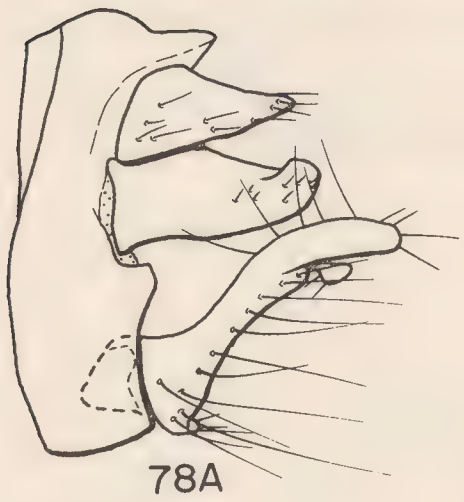


76C

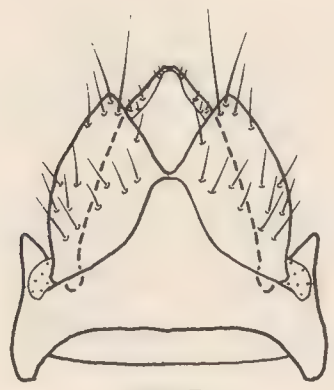
76D

77C

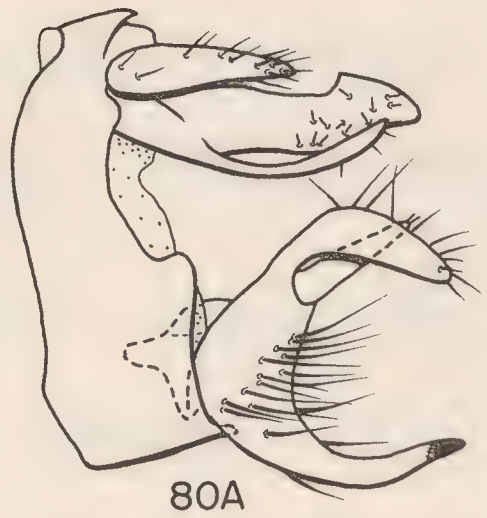
77D



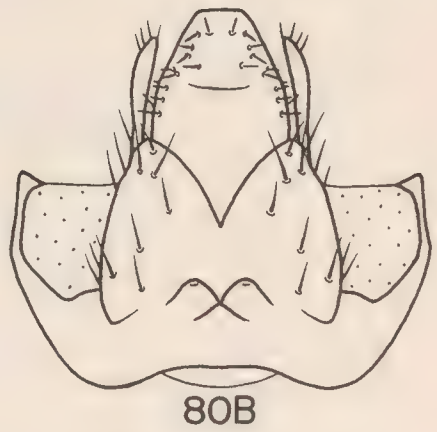
78A



78B

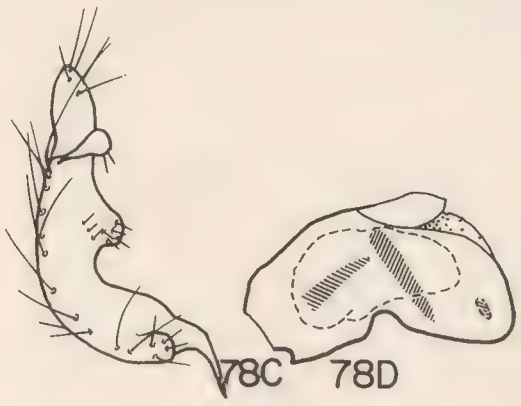


80A



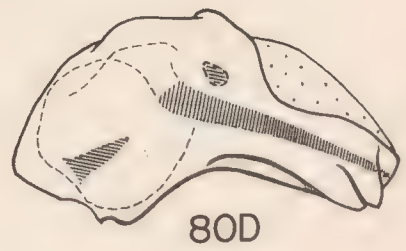
80B

79C



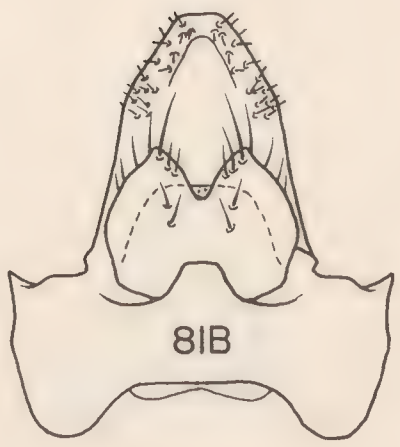
78C 78D

80C

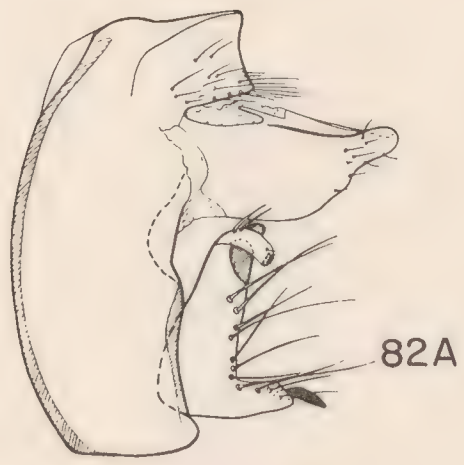


80D

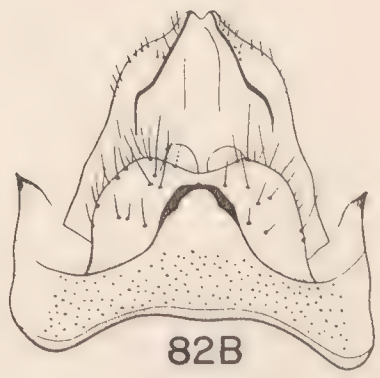
81A



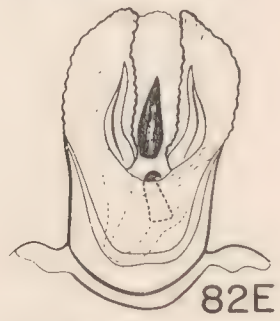
81B



82A

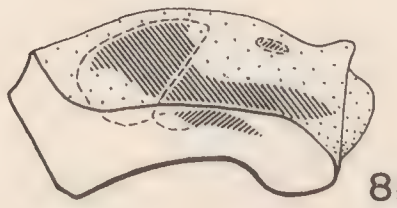


82B

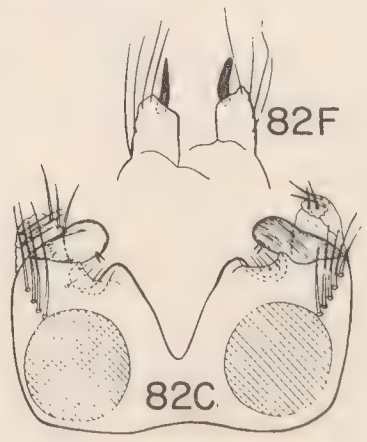


82E

81C



81D



82C 82F

82D

Figs. 83-87. Male genitalia of Ceraclea (Athripsodina) Annulicornis Group. A, left lateral. B, dorsal. C, inferior appendage, caudal. D, phallus, left lateral. E, same with endothecal membranes, paramere, and phalicata extruded, ventral.

Fig. 83. Ceraclea (Athripsodina) excisa (Morton), specimen from Finland.

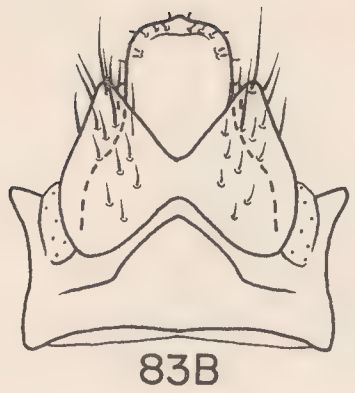
Fig. 84. Ceraclea (Athripsodina) annulicornis (Stephens), specimen from Oregon.

Fig. 85. Ceraclea (Athripsodina) ruthae (Flint), holotype.

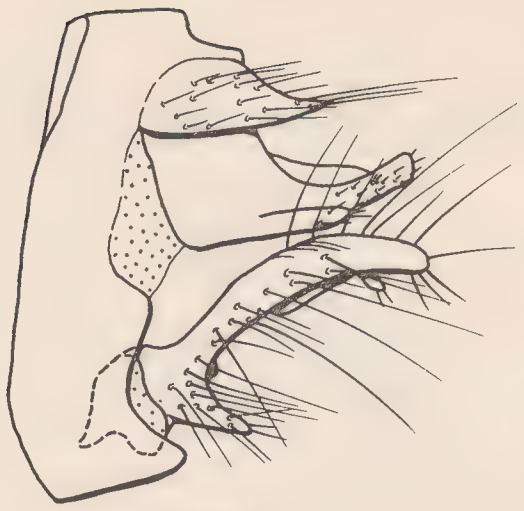
Fig. 86. Ceraclea (Athripsodina) bicalcarata (Schmid), paratype.

Fig. 87. Ceraclea (Athripsodina) shuotsuensis (Tsuda). (from Tsuda, 1942a)

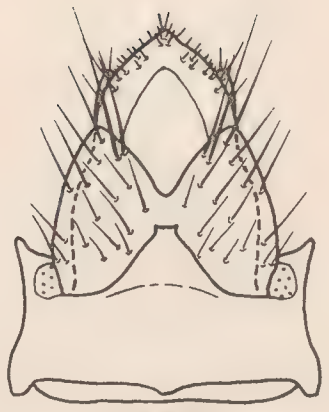
83A



83B

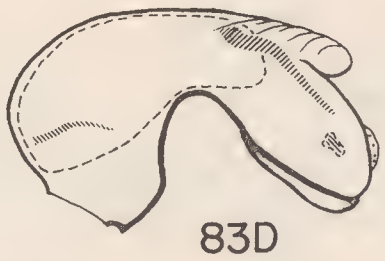


84A

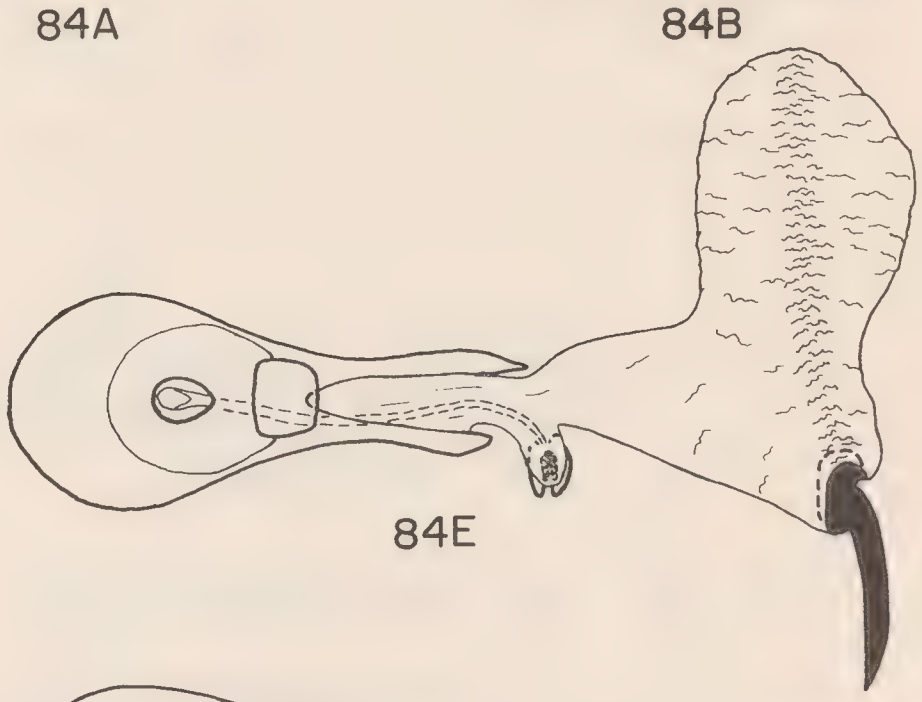


84B

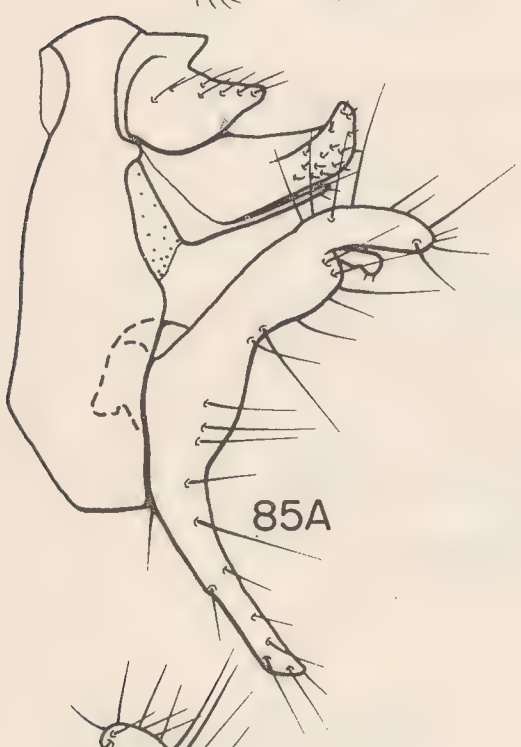
83C



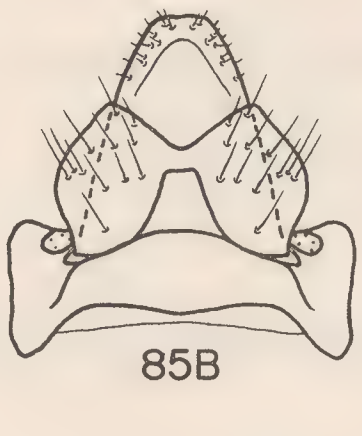
83D



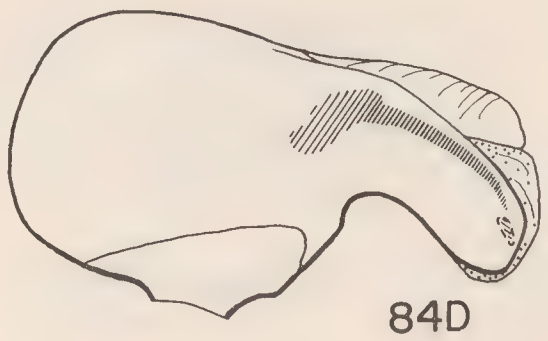
84E



85A

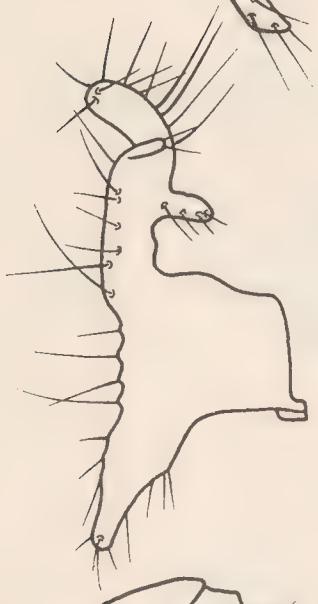


85B

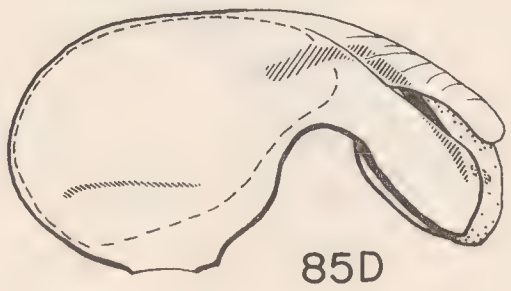


84D

84C



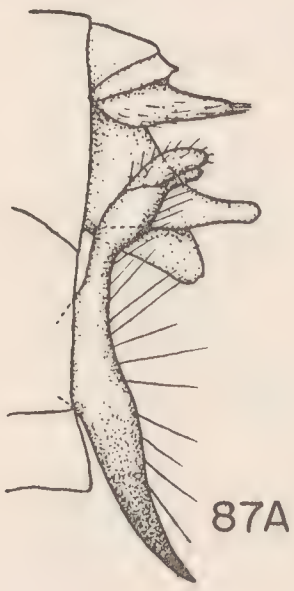
85C



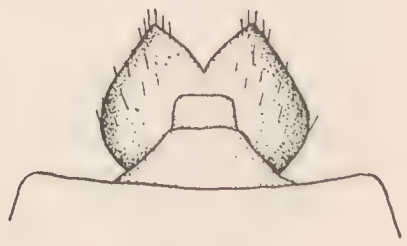
85D

86A

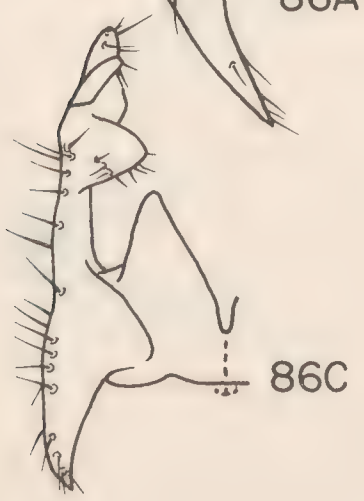
86B



87A



87B



86C

86D

Figs. 88-93. Male genitalia of Ceraclea (Athripsodina) Riparia Group. A, left lateral. B, dorsal. C, inferior appendage(s), caudal. D, phallus, left lateral.

Fig. 88. Ceraclea (Athripsodina) riparia (Albarda), specimen from France.

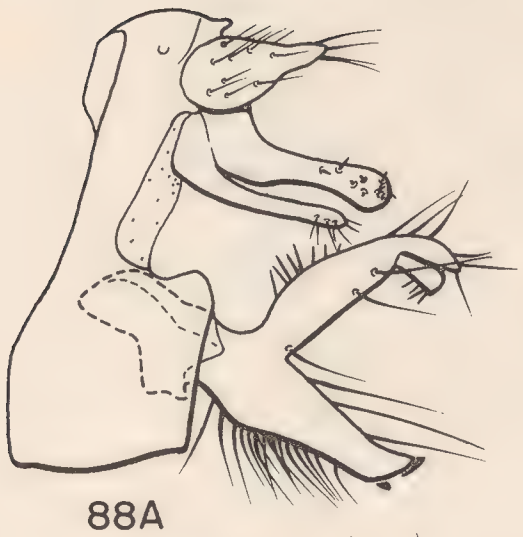
Fig. 89. Ceraclea (Athripsodina) yangi (Mosely), paratype.

Fig. 90. Ceraclea (Athripsodina) modesta (Banks); A, B, and D, paralectotype; C, lectotype.

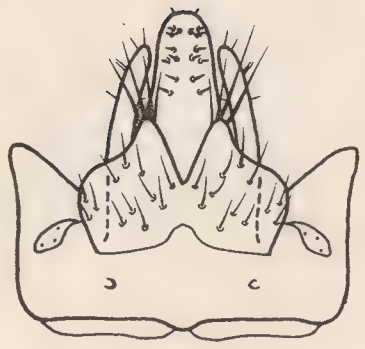
Fig. 91. Ceraclea (Athripsodina) isurumuniya (Schmid), specimen from Ceylon.

Fig. 92. Ceraclea (Athripsodina) forcipata (Forsslund), holotype.

Fig. 93. Ceraclea (Athripsodina) flava (Banks), specimen from Washington, D. C.



88A



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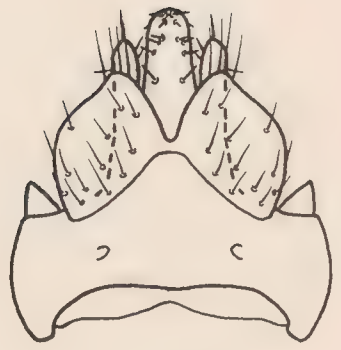

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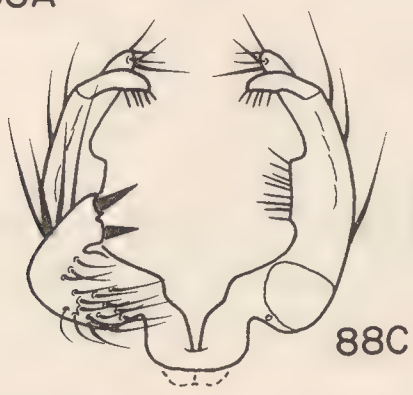

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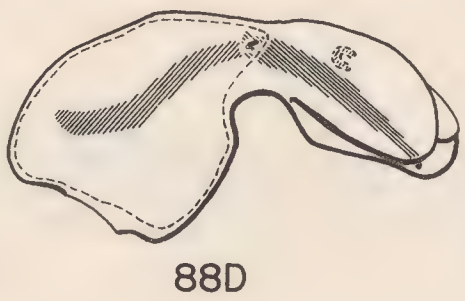

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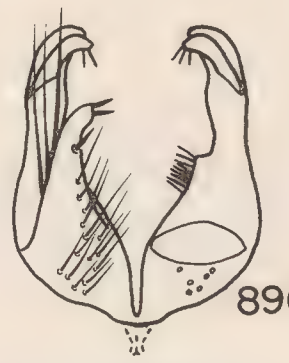

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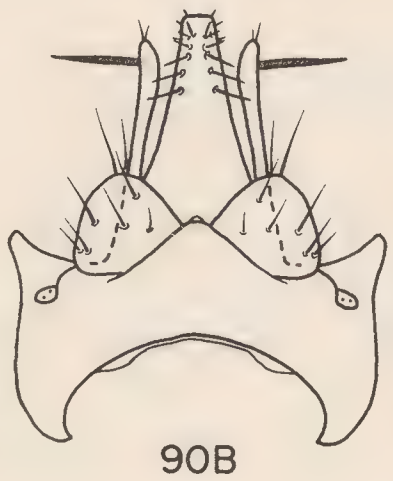

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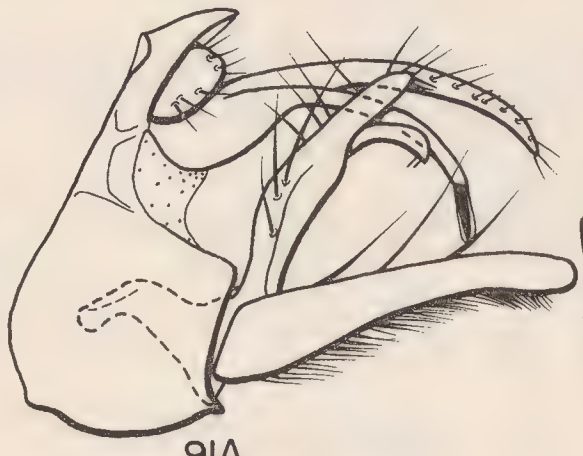

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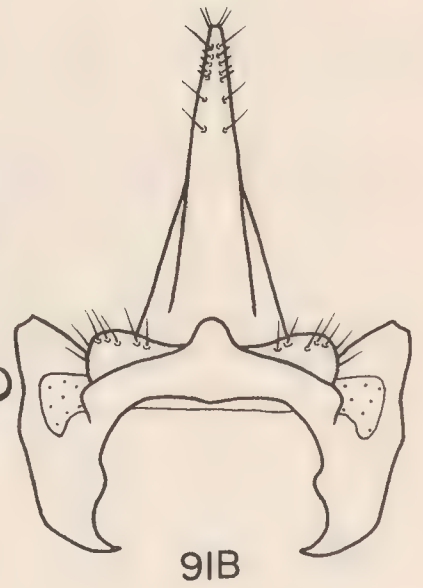

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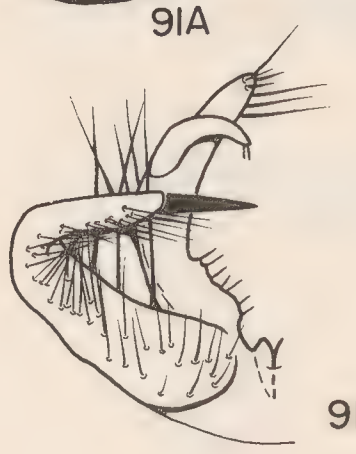

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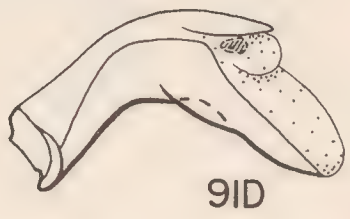

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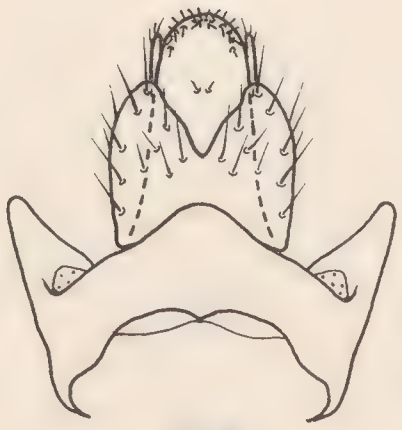

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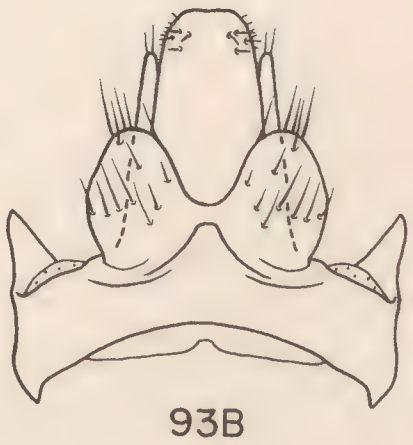

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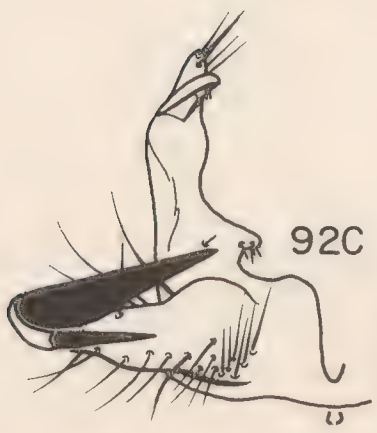

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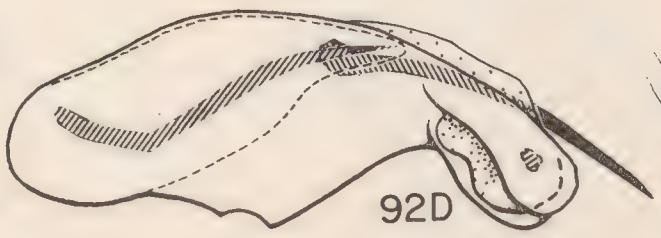

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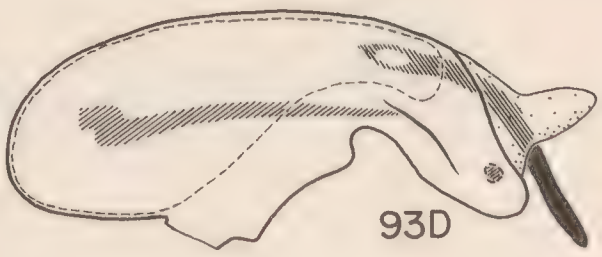

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Figs. 94-96. Male genitalia of Ceraclea (Athripsodina) Riparia Group; 97-99, Marginata Group. A, left lateral. B, dorsal. C, inferior appendage(s), caudal. D, phallus, left lateral.

Fig. 94. Ceraclea (Athripsodina) kamonis (Tsuda). (from Tsuda, 1942b)

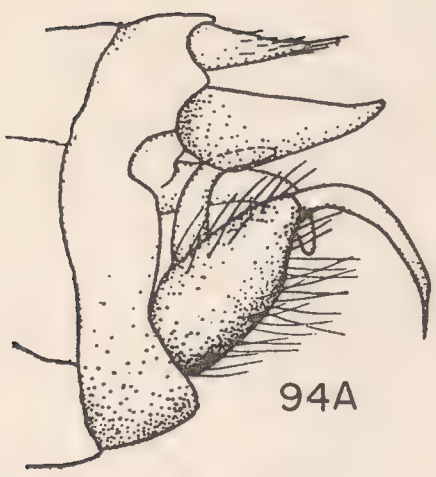
Fig. 95. Ceraclea (Athripsodina) ancylus (Vorhies); A, B, and C, specimen from Illinois; D, specimen from Manitoba.

Fig. 96. Ceraclea (Athripsodina) nankingensis (Hwang). (from Hwang, 1957)

Fig. 97. Ceraclea (Athripsodina) fooensis (Mosely), holotype.

Fig. 98. Ceraclea (Athripsodina) martynovi (Forsslund), specimen from Ceylon.

Fig. 99. Ceraclea (Athripsodina) marginata (Banks), specimen from type locality in India.



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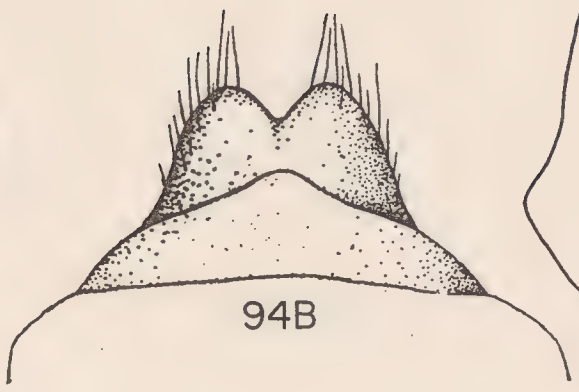

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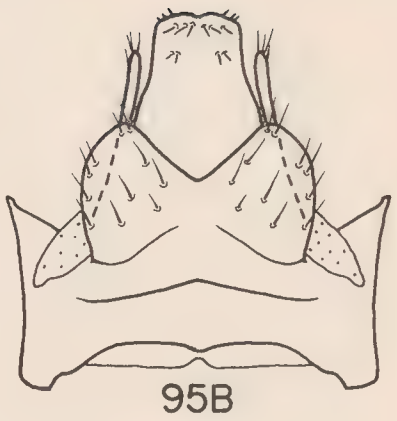

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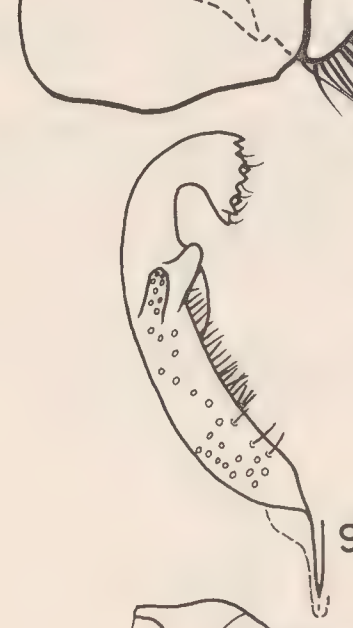

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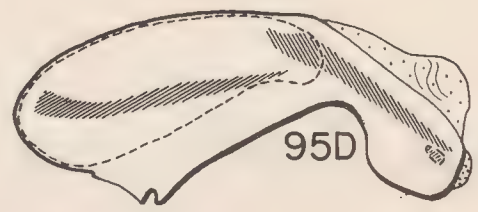

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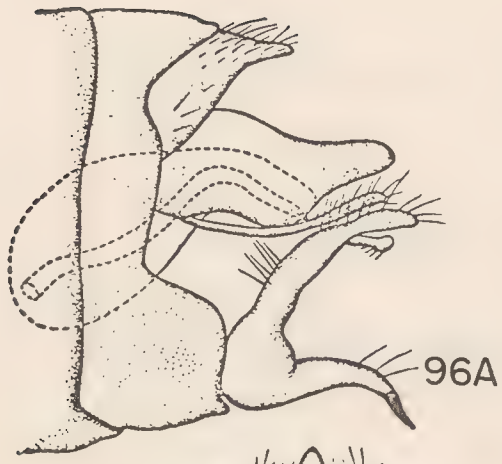

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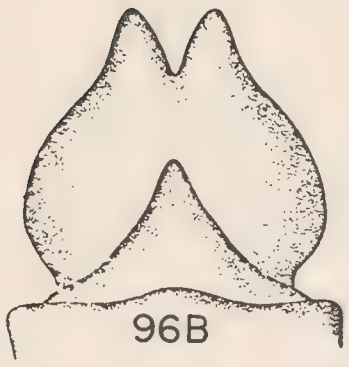

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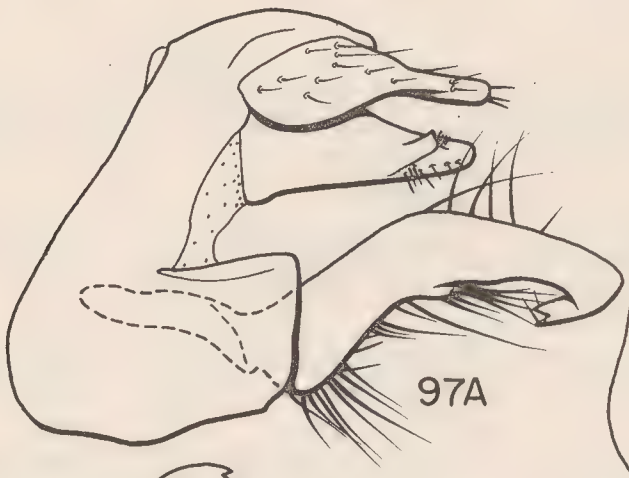

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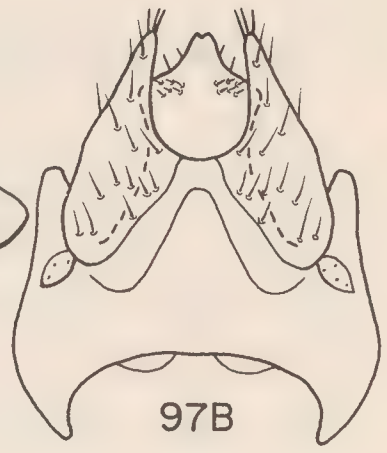

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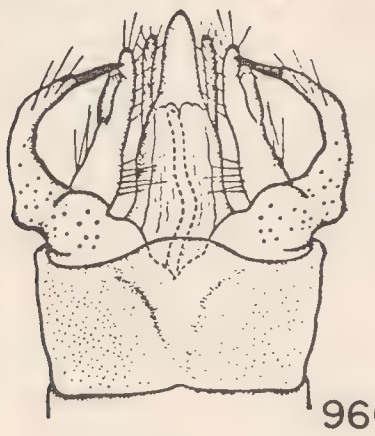

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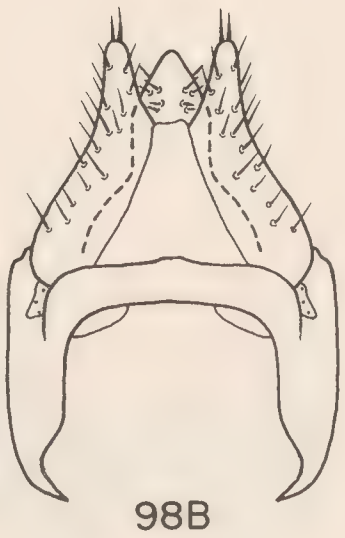

98B

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99B

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99D

Figs. 100-105. Male genitalia of Ceraclea (Athripsodina) unplaced and unexamined species. A, left lateral. B, dorsal. C, inferior appendage(s), caudal. D, phallus, left lateral. E, ninth sternum, ventral.

Fig. 100. Ceraclea (Athripsodina) dingwuschanella (Ulmer), specimen from Chekiang, China.

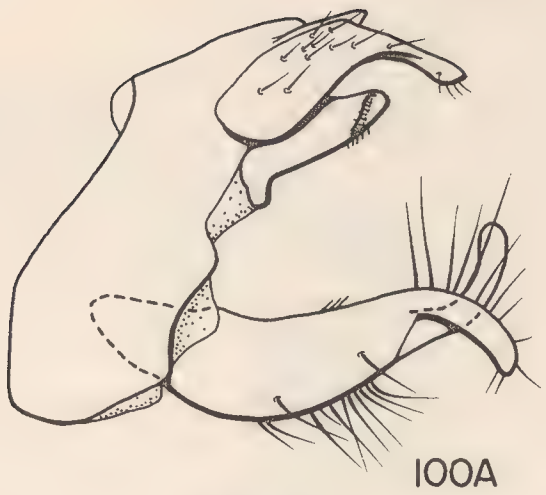
Fig. 101. Ceraclea (Athripsodina) ensifera (Martynov), paratype.

Fig. 102. Ceraclea (Athripsodina) kashingensis (Tsuda). (from Tsuda, 1943)

Fig. 103. Ceraclea (Athripsodina) kolthoffi (Ulmer), holotype.

Fig. 104. Ceraclea (Athripsodina) major (Hwang). (from Hwang, 1957)

Fig. 105. Ceraclea (Athripsodina) mitis (Tsuda). (from Tsuda, 1942b)



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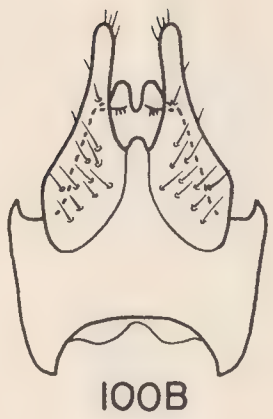

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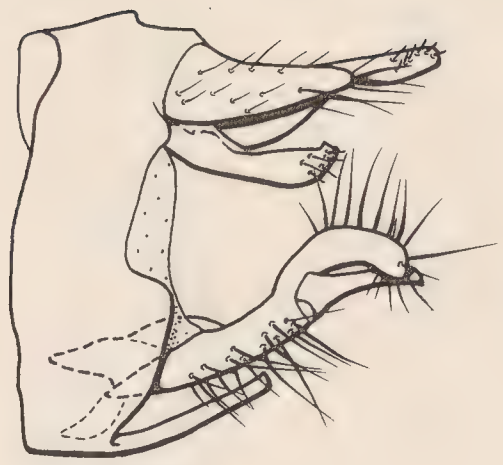

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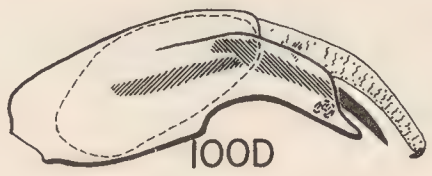

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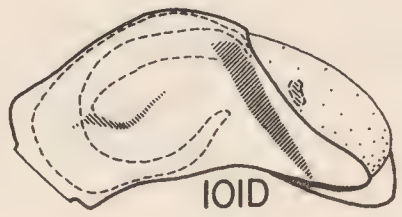

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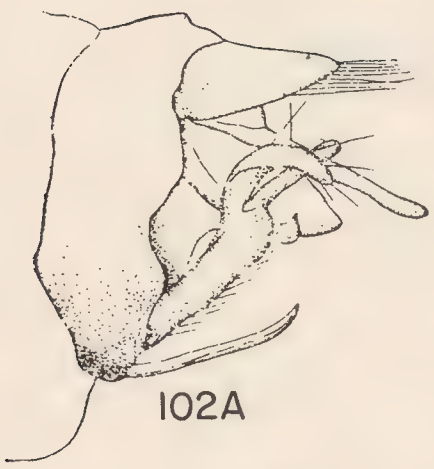

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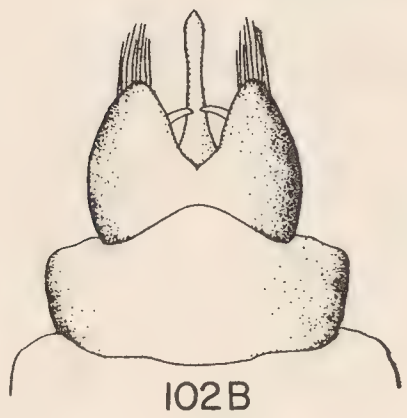

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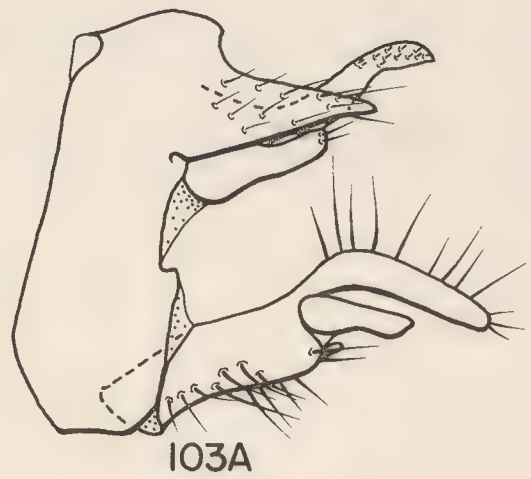

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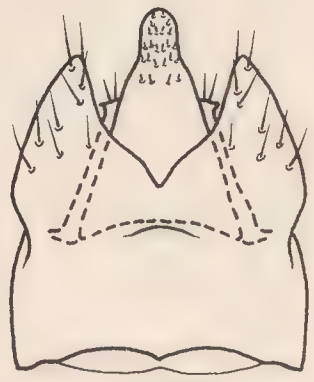

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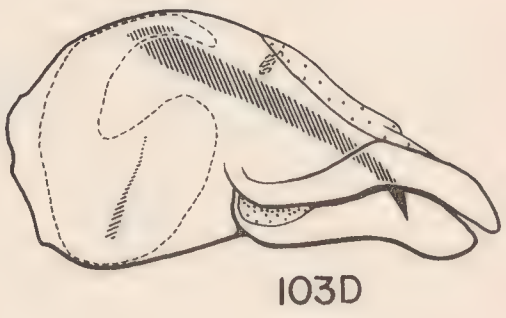

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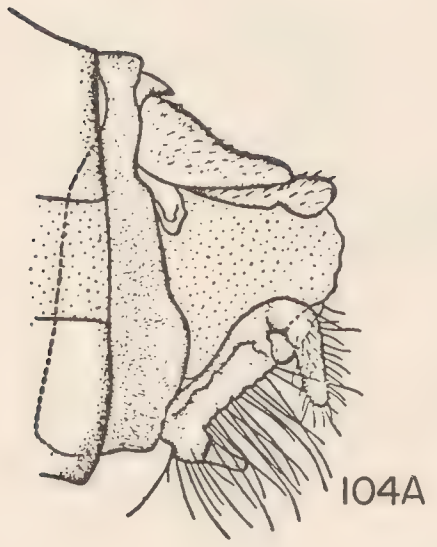

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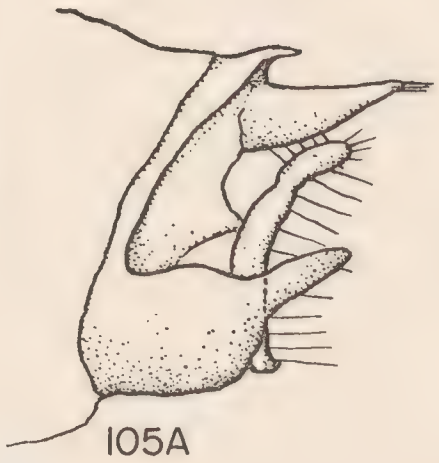

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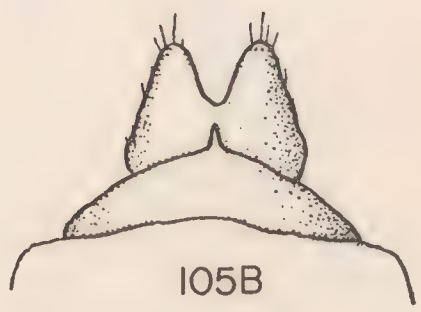

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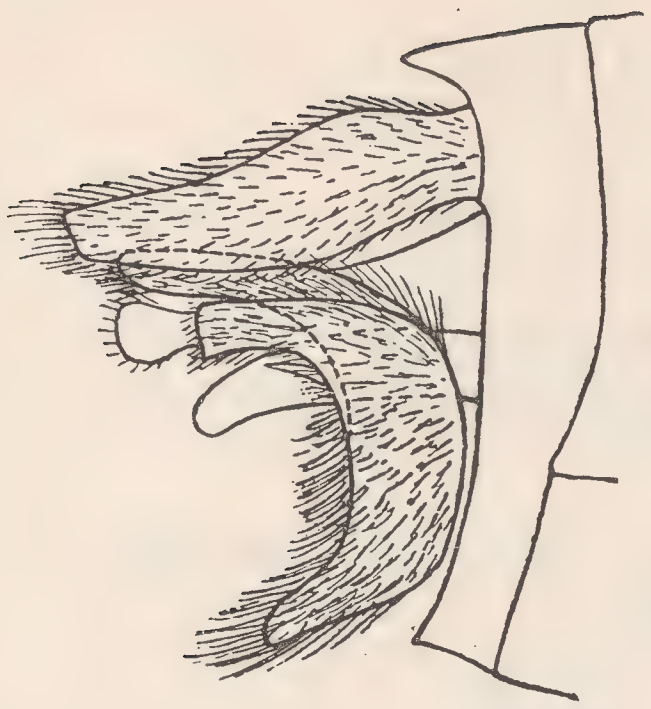
Figs. 106-108. Male genitalia of Ceraclea (Athripsodina) unplaced and unexamined species. A, lateral. B, dorsal. C, inferior appendage(s), caudal. D, phallus, left lateral.

Fig. 106. Ceraclea (Athripsodina) signaticornis (Ulmer). (from Ulmer, 1926)

Fig. 107. Ceraclea (Athripsodina) ungulifera (Kimmins), paratype.

Fig. 108. Ceraclea (Athripsodina) variabilis (Martynov), paratype.



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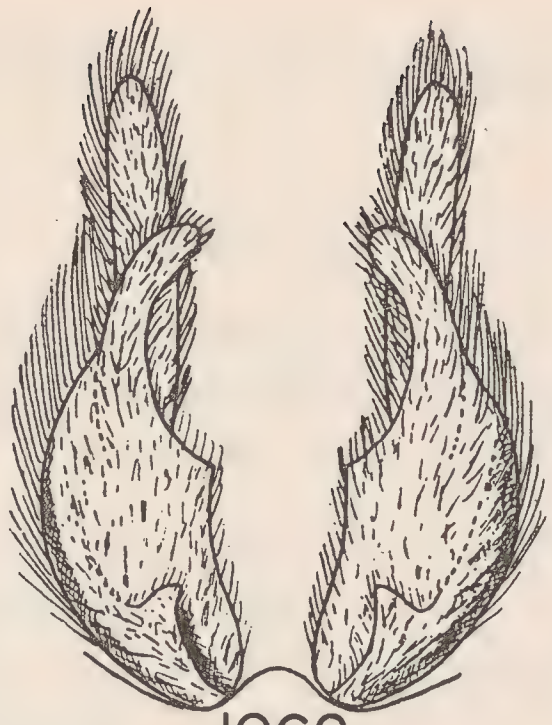

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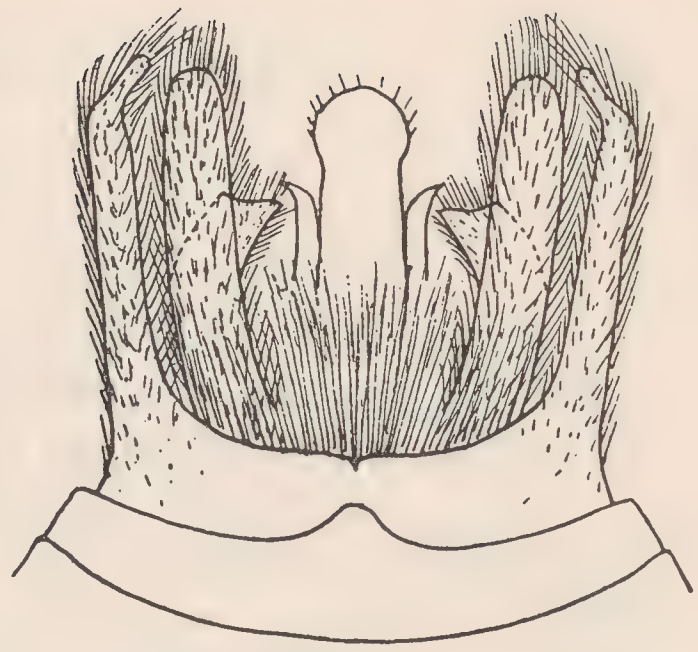

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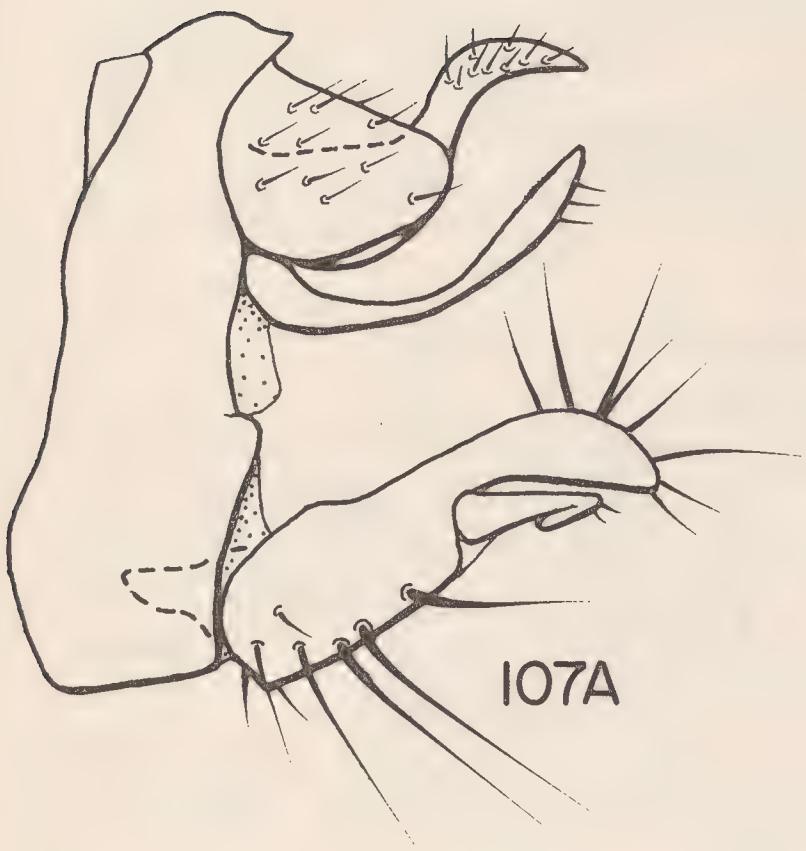

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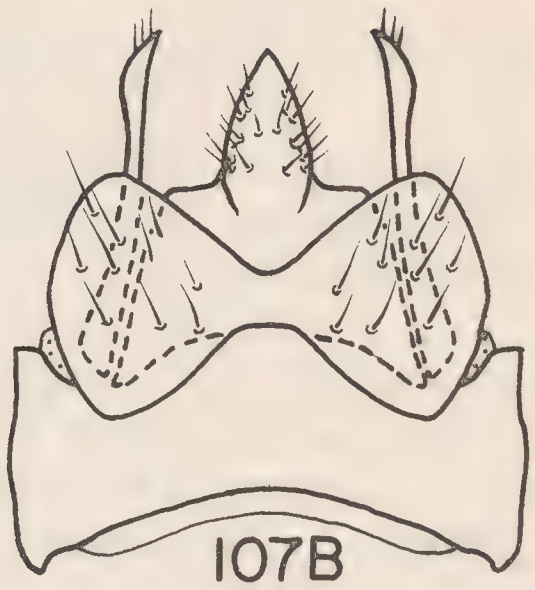

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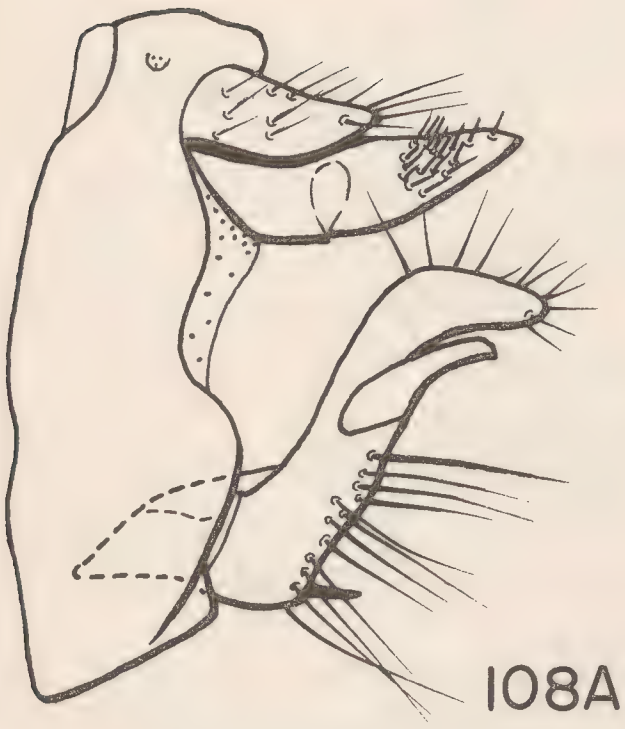

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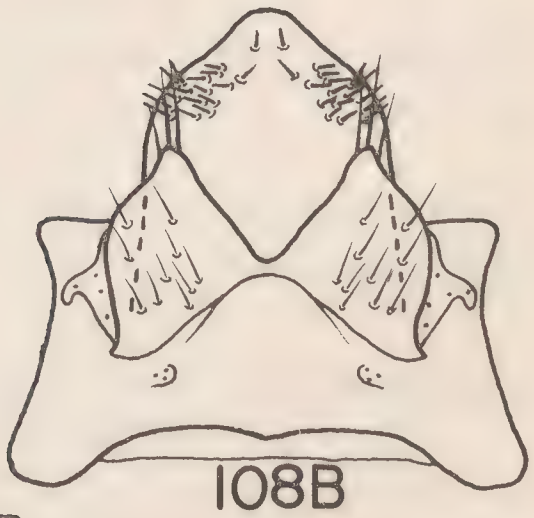

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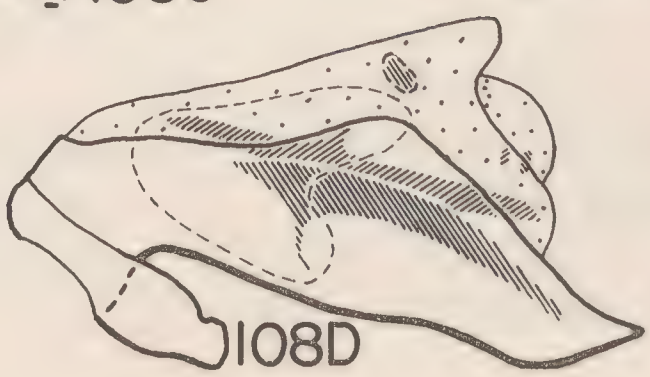

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